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FUNCTIONAL MORPHOLOGY OF THE MOUTHPARTS OF BLACKFLY LARVAE (DIPTERA : SIMULIIDAE)

by


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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled: Functional Morphology of the Mouthparts of Blackfly Larvae (Diptera : Simuliidae), submitted by Mary MacCrimmon Chance in partial fulfilment of the requirements for the degree of Master of Science.

Abstract

Blackfly larvae select their food entirely on the basis of size. The diameters of particles ingested by 4 filtering species: *Cnephia dacotensis* Dyar and Shannon, *Simulium decorum* Walker, *Simulium venustum* Say and *Simulium vittatum* Zett., range from less than one micron to about 350 microns; most commonly ingested particles ranged from 10 to 100 microns in diameter. The size distribution of ingested particles varied between species. Larvae of *Twinnia nova* (Dyar and Shannon), a non-filtering species, ingested particles of a similar size.

Differences in feeding among filtering species are not attributed to morphological differences. The mouthparts of filtering and grazing species are adapted for their respective modes of feeding.

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Autobiographical Sketch

After attending high school in Montreal and graduating from grade 11 (junior matriculation), I attended McGill University in Montreal for 4 years. I took the honours zoology program and graduated with first class honours in 1965. I was awarded the Fantham Memorial Prize in Zoology (McGill, 1965) and the Entomological Society of Alberta Prize (1966). While I have been attending the University of Alberta, the Ministry of Education, Quebec, awarded me an honorary scholarship for two years (1965-1967) and the National Research Council of Canada, a scholarship for 3 years.

During my final years at McGill, I decided to continue my university education by studying some aspect of invertebrate morphology. I became interested in entomology while taking a course in arthropod biology. In 1966, I spent a summer at the Entomology Research Institute in Belleville, working as a summer assistant to Dr. P. Belton. He was carrying out research on mosquitoes. While applying for acceptance into graduate school, I received information from Dr. B. Hocking (Department of Entomology, University of Alberta) concerning the interest of the World Health Organization in the biology of Simuliidae, specifically the feeding habits of larval blackflies.

Belton, P. and M.M. Galloway. 1966. Light-trap collections of mosquitoes near Belleville, Ontario, in 1965. Proc. ent. Soc. Ont. 96: 90-96.

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Introduction

Chemical control programs have been aimed at blackfly larvae for over 20 years. The most effective formulation is that of DDT adsorbed onto particles which blackfly larvae ingest along with their particulate food (Fredeen, Arnason and Berck 1953; Fredeen, Arnason, Berck and Rempel 1953; Kershaw et al. 1965). In order to understand better the effectiveness of DDT adsorbed onto particles, the World Health Organization sponsored this study on the feeding mechanisms of blackfly larvae.

The primary aim of the study was to determine what particle size blackfly larvae ingested. This would be helpful in developing a particulate formulation of DDT which is specific for blackfly larvae and less harmful to other aquatic fauna.

The study was conducted in two parts. The size of the particles ingested was investigated by feeding the larvae variously sized polyacrylic beads. The species variability in feeding was examined in a detailed morphological study of the mouthparts of the species involved.

1.0. LITERATURE REVIEW

1.1. Early Works on Simuliidae

Interest in Simuliidae was stimulated initially by the damage they cause to livestock and the suffering they cause to man. The earliest reports of blackflies in North America are those of Champlain in 1559 (*in* Biggar 1922, 1925), Sagard in 1632, Lahontan in 1703, and Agassiz in 1850. They describe the misery that adult blackflies inflicted on both Indian and white man. Barnard (1880) reported seeing the buffalo fly, known then to kill domestic animals, killing poultry in great numbers. Osten Sacken (1870) gave detailed reports of 13 species of blackflies on animals and man. In 1870 Riley reported that cultures of young trout were destroyed when the fry became caught in the silk web spun by *Simulium* larvae. McBride disputed this charge (*in* Osborn 1896).

In Europe, the Columbacz midge, *Simulium reptans* Lat., was reported as a major pest of livestock as early as 1679 (Osten Sacken 1870). It was the first species of *Simulium* to be studied in any detail. Schönbauer discovered the eggs and immature forms in running water in 1795 (Osten Sacken 1870, Puri 1925). According to Osten Sacken (1870) and Puri (1925), Eichorn illustrated the larvae of an unnamed species in 1774, but did not associate them with the adult. Reports of blackfly adults coming out of caves persisted for nearly a century (Tömösváry 1892 *in* Puri 1925, Letho 1880). Letho (1880) reported that he collected all stages of *Simulia golumbacensis* (= *S. reptans*), the 'Kolumbacs Fly', and noted that the life history of this species conforms to that of other Nematocera.

Early observations on the biology and morphology of the larvae were made by Verdat in 1822 (*Simulium ornatum*) Mg., Fries in 1824 and Westwood in 1848 (all *in* Puri 1925), Planchon (1844), Osten Sacken (1870), Riley (1870), Barnard (1880), Miall (1895) and Osborn (1896). These authors described the location, development and feeding habits of the larvae and the location and development of the pupae. Osborn's work concerned all stages of development and included material on control procedures and preventative measures against attack as well as notes on natural enemies. Kölliker (1842),Meinert (1886) and Mecznikow

(1886) reported embryological findings.

Newstead (1907) reported on the biology of *S. ornatum* larvae, Jobbins-Pomeroy (1916) and Cameron (1922) reported on the biology of immature and mature forms in North America, and Edwards (1921) reported on British *Simulium* larvae. Kellogg (1901) mentioned the food of Simuliidae and Blepharoceridae. Taylor (1902) studied the tracheal system of larvae, pupae and adults. Strickland (1911) studied the effects of parasitism on larval development. Puri (1925) produced the first major morphological work on blackfly larvae. Debot (1932) described the silk apparatus and salivary glands of the larvae. Gambrell (1933) reported on the embryology of *Simulium pictipes* Hagen. Fortner (1937) gave a comprehensive report on the feeding behaviour of blackfly larvae.

With Blacklock's (1926) discovery that blackfly adults are the vectors of onchocerciasis, the incentive for work on Simuliidae was greatly increased. De Meillon (1930) and Gibbins (1933) began studies on the Ethiopian blackflies; Smart (1934, 1944) worked on British forms; Wu (1931) and Metcalf (1932) studied North American species. Grenier (1949) described the biology of the blackflies of France. Dalmat (1955) gave a comprehensive account of Guatemalan blackflies and their relation to onchocerciasis. Ussova (1964) and Rubtzov (1964) worked on Russian blackflies.

Major accounts of the ecology of simulid larvae were given by Peterson (1956), Zahar (1957), Davies and Syme (1958), Anderson and Dicke (1960), and Carlsson (1962, 1967). Anderson and DeFoliart (1962) and Phelps and DeFoliart (1964) described in detail mermithid parasitism of larval blackflies. Welch (1964) reported on parasitism by mermithids and discussed its uses as a method of control. Fredeen (1960, 1964) and Williams et al. (1961) described food particles ingested by larvae.

1.2. Morphology

1.2.1. Morphology of Nematocera

The majority of morphological studies carried out on Nematocera have been directed

towards elucidating the relationship of the Diptera to other orders of the panorpoid complex (Hinton 1958a) and towards interpreting the structure of the mouthhooks of larval Cyclorrapha (Cook 1949).

Some of the earlier works on the morphology of Nematocera are those of Johannsen (1903) who discussed representatives of most nematocerous families. Miall and Hammond (1900) studied chironomids. Morris (1921) described the larval and pupal stages of bibionids, but did not attempt to make any homologies. Wardle and Taylor (1926) described the mouthparts of tipulids.

Hinton (1958a) discussed the mouthparts of larval Nematocera in comparison with those of other orders of the panorpoid orders.

The mouthparts of insects are discussed and earlier works reviewed by Snodgrass (1935), Das (1937), and most recently and comprehensively by Matsuda (1965).

Anthon (1943) produced a detailed description of the morphology of a species of Anisopodidae. Lawson (1951) described the early stages of a ceratopogonid. Nowell (1951) studied the structure and function of the mouthparts of larval dixids in western North America. In 1955 Chiswell described the anatomy of the head of the last instar of a tipulid species.

In a series of papers, Cook (1944a, b, c, 1949) reported on a comprehensive study on the anatomy of representatives of nematocerous and brachycerous flies. His works are an important contribution to the understanding of the evolution of dipterous larval heads, although many of his terms and homologies have been disputed (Shalaby 1951, Menees 1958a, b, Snodgrass 1959 and Chaudonneret 1962, 1963). Shalaby, Snodgrass and Menees studied mosquitoes. Chaudonneret worked on midges and dixids as well as mosquitoes. These authors have argued at length on the interpretation of various parts of the larval mosquito head capsule and mouthparts, in particular the presence or absence of 'premandibular' structures, the tormae, messores and the homologies of the labium. In 1962 Pucat worked on the functional morphology of the larval mosquito mouthparts. Her review on the morphology of larval mosquitoes is comprehensive.

1.2.2. Morphology of Simuliidae

Puri (1925), Fortner (1937) and Grenier (1949) produced major morphological studies of the mouthparts of blackfly larvae. Puri described the external and internal anatomy of the larva and pupa of *Simulium nolleri* Fried. He also described the morphology of 16 other species of blackflies and the first instar of both *Simulium erythrocephalum* De G. and *Simulium aureum* Fries., all classified at that time as members of the genus *Simulium*. Fortner (1937) described in detail the activity of the cephalic fans and the feeding behaviour of an unidentified species of larval blackfly. Grenier (1949) devoted a chapter of his monograph to the cephalic fans. He discussed the homologies of the fans as well as their structure and function. He disagreed in part with both Puri and Fortner on their interpretation of the origins and movements of the fans.

Rubtzov (1964) described the cephalic fans and mandibular brushes. However, he did not describe the movement of the fans or the mouthparts, nor did he attempt to homologize any of the structures.

The cephalic fans have attracted much of the attention of later workers. In a taxonomic work, Sommerman (1953) described two arrangements of the secondary fan which are now used as criteria to separate genera of Simuliidae. In 1960 Crosskey produced a taxonomic work and his discussion of the terminology applied to larval head structures is valuable. His section on changes of certain head structures between instars is useful.

Dumbleton's work (1962b) on blackfly species of the southern hemisphere is an important contribution to the morphology and the study of simuliid phylogeny. He discussed the most commonly used taxonomic characters of pupae and larvae of both hemispheres. Dumbleton (1962a) described the unusual larvae of the insular forms *Crozetia crozetensis* (Womersley) and *Simulium oviceps* Edwards, both of which have abnormal cephalic fans. On the basis of adult and larval morphology, he considered both species to be either degenerate or specialized rather than primitive. He considered larvae of *Gymnopais* Stone and Jamnback and *Twinnia* Stone, which lack cephalic

fans, to be primitive and closely related to *Prosimulium* larvae. He maintained that the Australasian genus *Austrosimulium* is more closely related to *Simulium* than to *Prosimulium* (Dumbleton 1962a). He (1964) described the first instar of a species of *Austrosimulium.*

In 1960 Davies was the first to describe the first instar of a species of *Prosimulium*, probably *P. fuscum* Syme and Davies. It lacks cephalic fans even though these are completely formed in the second instar. He suggested that this occurs throughout *Prosimulium.* The absence of cephalic fans from *Prosimulium* first instars is claimed by Davies to confirm the primitiveness of *Prosimulium* and hence its close relationship to *Twinnia* and *Gymnopais*. In 1965 Davies described the first instar of a *Twinnia* and a *Gymnopais* species. He discusses their relationship with *S. oviceps* and *Crozetia crozetensis*. He considers *C. crozetensis* more highly developed than *Gymnopais, Twinnia* and *Prosimulium* but not as well developed as *S. oviceps* with respect to feeding mechanisms. His view contrasts with that of Dumbleton.

Wood (1963) studied the cephalic fans and their movements. He described the fans of the first instar of *Simulium pictipes*. In discussing the phylogeny of blackflies, he concluded that *Prosimulium* is the most primitive, that *Gymnopais* and *Twinnia* larvae have secondarily lost their cephalic fans and that *S. oviceps* larvae have reduced cephalic fans.

The silk producing activity of blackfly larvae has not attracted much attention. Puri (1925) described the salivary (silk) glands and their opening, but did not describe how the silk strand was expelled from the mouth. Debot (1932) produced a precise description of the morphology and activity of the silk apparatus. Grenier (1949) gave a comprehensive description of the silk glands, silk canal and press. Wood (1963) suggested that the hypostomial teeth may be used to cut the silk thread.

1.3. Filter Feeding

The early classifications of animals according to their manner of feeding were comprehensively reviewed by Younge (1928). The most recent review of filter feeding is that of Jørgensen (1966), a marine biologist. The greater part of his book deals with marine invertebrates, however he includes most of the work concerning insects. He discusses the terms suspension feeder, filter feeder and deposit feeder. A suspension feeder, as originally defined by Hunt (1925), is one which selects from the surrounding water suspended microorganisms and detritus (*in* Jørgensen 1966). The use of the word 'selects' is unfortunate because suspension feeders select only with respect to physical properties of particles and not with respect to quality of food. Filter feeders obtain food by passing surrounding media through structures that retain particles mainly according to size and shape. Jørgensen modifies Hunt's definition by describing active and passive filterers. Active filterers create their own feeding current; passive filterers live in flowing waters and rely on the current to bring them food. Jørgensen (1966) considers deposit feeders to have evolved from suspension feeders. Various filter feeding methods of chironomids support this idea.

Jørgensen discusses the mechanical aspect of filter feeding to a greater extent than earlier workers. Filter feeding tends to be very automatic. It is characterized by a continuous and steady flow of water to the structures that retain the suspended particles. Jørgensen states that the accumulation of food proceeds at a rate independent of need but dependent on the rate of water flow past the filtering mechanism. This applies whether the transport is active or passive. Food accumulation also depends on the concentration of food in the water and the efficiency of the filter in retaining particles. Jørgensen discusses the porosity of filters which tends to be coarser among freshwater insects than marine animals.

Among insects, filter feeding has evolved independently several times (Jørgensen 1966). Hartland-Rowe (1953) described the mode of feeding of *Povilla adusta* Navas,

a lake dwelling ephemeropteran, and compared it with that of rheophilic ephemeropterans. Feeding in trichopterans was discussed by Wesenberg-Lund (1943). The influence of the current on construction of feeding nets of trichopterans has been studied by Kaiser (1962), Ambühl (1959) and Jaag and Ambühl (1964). The last two authors also discuss the effect of current boundary layers on aquatic insects.

Feeding in chironomids has been studied by Miall and Hammond (1900), Burtt (1940) and Walshe (1947, 1951). Filter feeding by the leaf mining chironomid was described by Burtt (1940), and by the mud-dwelling chironomid, by Walshe (1947). In 1951 Walshe described 3 types of feeding methods among chironomids: that of *Tendipedes plumosus* L., of *Rhectanytarsus* sp. and that of 5 species of leaf mining chironomids. She suggested that the 3 types were independently evolved.

Although Jørgensen mentions simuliids, he omits dixids and culicids. Nowell (1951) described filter feeding by dixids. Filter feeding by mosquitoes has been studied by Wesenberg-Lund (1943), Bates (1949), Pucat (1962) and many others. Renn (1941) described in detail filter feeding by anopheline mosquitoes. He carried out comparative studies on feeding and also reported similar findings by Senior-White (1928). Surtees (1959) proposed a classification of mosquito larvae according to 3 feeding habits: filter feeding, browsing, and predation. He listed structural developments for all types.

1.4. Feeding Methods of Simuliidae

The earliest descriptions of the cephalic fans have always associated these organs with the role of food-getting. Although Barnard in 1880 suggested a mechanism by which the fans catch food, the accomplishment of this was not made clear until Strickland (1911) described the flicking motion of the fans.

In 1870, Riley stated that the cephalic fans act either by spreading silk nets spun by the larvae which thereby catch 'animalcules' for food, or, by creating a current of water by which food is drawn towards the mouth. Osten Sacken (1870) attributed a food-getting role to the cephalic fans; he did not describe this role but suggested that the brushes of the mandibles are used for cleaning the fans. Miall (1895) also reported

this cleaning process. Barnard (1880) thought that the fans rake food particles from the water and into the mouth. Osborn (1896), describing the habits of *Simulium pecuarum* Riley, stated (page 45):

> "To obtain these (food particles) the fan-like organs peculiar to these larvae create currents of water directed towards the mouth. Any small and floating matter drifted by the current of water into the vicinity of these fans is attracted by the ciliary motion of the component rays of the same and thus reaches the space embraced by them, and they, bending over the mouth, direct the further motion of the particles."

Strickland (1911) observed the filtering operation of the fans and stated that any current-creating activity would be useless in a habitat of swiftly running water. He was also the first to report the existence of two large glands; he suggested that they secrete a mucous film which aids in the cleaning of the cephalic fan rays. Jobbins-Pomeroy (1916), Cameron (1922) and Puri (1925) all refuted the current-creating activity of the fans. Puri studied their flicking motion and noted that they closed alternately, while the labrum is 'drawn out' and the mandible and maxilla retracted. He also stated that the food particles are passed from the fans to the other mouthparts.

Fortner (1937) gave a comprehensive account of the activity of the fans and the transfer of food from the fan rays to the labrum and the mandibles. Both she and later Harrod (1965) discussed the influence of water currents on the movements of the fans. The filter feeding mechanism is also described by Smart (1944), Grenier (1949), Peterson (1956), Anderson and Dicke (1960) and Maitland and Penny (1967) among others.

Simuliid larvae have a second manner of feeding. They are capable of scraping material from the substratum. Both *Twinnia* and *Gymnopais* are believed to feed by scraping the substratum (Wood 1963). This has been observed among *Simulium* larvae equipped with cephalic fans (Puri 1925, Badcock 1949, Peterson 1956, Zahar 1957 and others). Dumbleton (1962a) suggested that *C. crozetensis* rakes food from the substratum with its atypical fans. He supported this view by finding filamentous algae in the gut contents of the larvae. He stated that the rays of the cephalic fans of

S. oviceps form an efficient filter. Davies (1960) did not report the first instar of *Prosimulium* feeding. Puri stated that scraping takes place occasionally and this is achieved by the mandibles. Wu (1931) reported this behaviour in the laboratory and regarded it as an artifact of the rearing conditions. His view is supported by later workers. Smart (1944) attributes it to larvae starving in the laboratory. Zahar (1957) stated that the larvae are almost entirely dependent on the cephalic fans for feeding and that they will only resort to substratum feeding under adverse conditions, stagnant or slow water for example. Badcock (1949), however, stated that scraping is quite common under natural conditions when the plankton is not very rich. Peterson (1956) observed scraping in the field and maintained that it is a normal way of augmenting the food supply.

In 1916 Jobbins-Pomeroy described the first instars of a *Simulium* species feeding on the matrix surrounding their eggs by scooping it up with their prolegs and thrusting it into their mouthparts.

1.5. Food Supply

There are many reports on the food of blackfly larvae, beginning with the earliest morphological reports (Puri 1925). Early workers tried to classify the larvae as herbivores or carnivores, whereas the larvae will eat anything of a suitable size that comes their way (Grenier 1949, Peterson 1956, Anderson and Dicke 1960). Fries (1824) considered blackfly larvae as herbivores (*in* Puri 1925). McBride and Riley thought that they fed on 'animalcules'(*in* Riley 1870), as did Osten Sacken (1870) and Planchon (1844). Osborn (1896) said that they eat animalculesbut did not reject pieces of vegetable matter. Jobbins-Pomeroy (1916) reported that they grow best in waters rich in *Euglena* sp. and *Spirogyra* sp., a claim contradicted by Cameron (1922).

Puri (1925) attributed differences in the reports of food to differences in collection localities. Grenier's work (1949) supported this idea. Grenier showed that mountain stream fauna ate less plankton than low altitude, slow river fauna as the mountain streams had a poorer plankton population. In a series of papers, Jones (1949a, b, 1950, 1951, 1958) demonstrated that the food of blackfly larvae depends on what is

available in the waters. "The very abundance of plant matter may force a phytophagous insect to eat it (Jones 1949b)." In two areas of Wales, several different species at the same locality all had similar gut contents (Jones 1949b). Peterson (1956) reported slight differences, mainly in his 'miscellaneous' category of food, between the gut contents of larvae attached to vegetation and those of larvae attached to rocks. He also showed differences in the same category of food between two creeks. Maitland and Penny (1967) found no differences in the gut contents of *Simulium equinum* L., *S. ornatum* and *S. reptans* found in the same locality.

Miall (1895) was the first to list inorganic material (sand) in the gut contents. Badcock (1949) reported finding no protozoans or mineral particles in larval guts. In contrast, Anderson and Dicke (1960) reported 76% - 85% inorganic contents. Abdelnur (1966) reports 100% soil particles in some larval guts.

The gut contents of simuliid larvae are a good indication of the particulate matter in the surrounding water; the larvae are unselective with regard to quality of their food. Osborn (1896) was wrong in his statement: "If of the proper kind, they (food particles) are eaten, otherwise they are expelled by a sudden parting of the fans." Jobbins-Pomeroy (1916) reported larvae as rejecting large paramecia and accepting only small phytoplankton. Smart (1944) described size as the only criterion for selection. This assumption is supported by the fact that larvae ingest a large amount of non-nutritive material including silt and probably the parasitic stages of mermithid and protozoan parasites.

In rearing experiments, simuliid larvae have grown well on a diet of vegetable matter and cultures of the protozoan *Polytomella coeca* Pringsh (Grenier 1949). Baker's yeast has also been used successfully (Fredeen 1959, Wood and Davies 1965, Abdelnur 1966). Fredeen (1960, 1964) studied the value of bacteria as food for larvae in both natural and field populations.

There are conflicting reports about the cannibalistic nature of blackfly larvae. Smart (1944) stated that larger larvae eat smaller ones. Badcock (1949) and Maitland and Penny (1967) stated that blackfly larvae occasionally eat their own species. Jones (1949b)

reported seeing no attacks of cannibalism. Wu (1931) stated that larvae in stagnant water eat dead larvae.

Williams and his co-workers (1961) investigated the sizes of particles ingested by *Simulium* larvae in the field. Their observations are tabulated below:

Table 1. Size in microns of particles ingested by blackfly larvae (from Williams et al. 1961).

Species	Particle size	
	longest axis	shortest axis
S. ornatum (location A)	11.3 ± 1.8	6.6 ± 1.7
S. ornatum (location B)	13.2 ± 2.1	7.3 ± 1.8
S. reptans	15.1 ± 2.0	8.0 ± 1.8
S. variegatum	14.8 ± 2.1	7.8 ± 1.9
S. tuberosum	12.0 ± 1.9	7.7 ± 1.9
early instars sp.	14.0 ± 1.7	7.3 ± 1.7

The gut contents of larvae reported by various authors are shown in table I of the appendix. Estimates of sizes are listed alongside.

1.6. Control Methods

The control methods aimed at blackflies have been mostly chemical. Since it was developed as a practical method, chemical control has been used against blackfly larvae. Various compounds have been tested as *Simulium* larvicides (Cope et al. 1947, Kindler and Regan 1948, Gjullin et al. 1949, Hocking et al. 1949, Hocking 1950, Travis et al. 1951, Lea and Dalmat 1954, 1955a, b, Muirhead-Thompson 1957, Jamnback and Eabry 1962, Travis and Wilton 1965, Guttman et al. 1966, Jamnback and Frempong-boadu

1966, Travis and Guttman 1966). In all tests, DDT (1, 1, 1 trichloro-2,2 bis (ρ -chlorophenyl) ethane) was the most satisfactory. Fairchild and Barreda (1945) were the first to use it. Using DDT, Garnham and McMahon (1947) eradicated *Simulium neavei* Roubaud in Kenya, where it was the onchocerciasis vector. These and subsequent control programs in Africa and South America are reviewed by McMahon (1966).

Until 1960 DDT was used to the exclusion of all other chemicals for effective *Simulium* control. Research had been concerned mainly with the formulation of DDT and its mode of application. DDT has been applied in oil solutions (Hocking et al. 1949, Barnley 1958, Hoffmann 1959), emulsions and wettable powders (Tiller and Cory 1947, Fredeen, Arnason and Berck 1953, Fredeen, Arnason, Berck and Rempel 1953, Lea and Dalmat 1955b, Kershaw et al. 1965), solutions in acetone (Cope et al. 1947, Gjullin et al. 1949), solutions in xylene or toluene and Triton X-100 (Hocking et al. 1949), in suspension (Travis and Wilton 1965), and in cakes of plaster-impregnated sawdust bags (Fairchild and Barreda 1945). The emulsified form produces the most satisfactory results (Jamnback and Frempong-boadu 1966). In aerial applications, a fuel oil solution is best (Hocking 1950). Spectacular results have been achieved using DDT adsorbed onto solids which form a suspension when put into streams (Fredeen, Arnason and Berck 1953, Fredeen, Arnason, Berck and Rempel 1953, Fredeen 1962).

The popularity of DDT as a *Simulium* larvicide is based on its great toxicity for blackflies but not for other stream fauna and its wide safety margin between insect and mammalian toxicities. Larvae are killed at very small concentrations (0.050 to 0.025 ppm), depending on stream conditions. A dosage of 0.10 ppm over an exposure time of 15 to 60 minutes is usually applied.

Despite the selective toxicity of DDT for Simuliidae, other members of the stream fauna are affected. Many of these animals are also the most susceptible to other candidate compounds for use as blackfly larvicides. Up to 80% reductions are recorded in populations of mayflies, stoneflies and caddisflies (Arnason et al. 1949, Corbet 1958, Hynes 1960,

Hynes and Williams 1962). Garnham and McMahon (1947) reported that many invertebrates and fish were destroyed. Hoffmann and Merkel (1948) reported reductions of 61% and of 90% of the stream fauna for 5 miles downstream from application. Hoffmann and Drooz (1953) found 70% to 90% reduction of fish foods. Gjullin and his co-workers (1949) found 90% to 100% mortality of caddisflies. Hocking and his co-workers (1949) recorded deaths in 37 families of stream fauna. Hynes and Williams (1962) reported the elimination of species of mayflies, ostracods, beetles and 3 families of flies. Jamnback (1962) found a reduction of mayflies and water mites.

Blackflies and mayflies reappeared in treated streams within a year (Garnham and McMahon 1947, Hoffmann and Merkel 1948, Hoffmann and Drooz 1953). They were the most numerous after repopulation (Hoffmann and Merkel 1948, Hynes and Williams 1962). This increase in their numbers is attributed to the absence of predators and shows how easily a single application of DDT can lead to an outbreak of blackflies (Davies 1950).

In comparison, in a 10-year program, DDT had little effect on some arthropods (Collins and Jamnback 1958, Jamnback and Eabry 1962). After years of use of DDT in the streams, the populations of mayflies, flies and water mites differed significantly between treated and untreated streams; but populations of beetles, dragonflies, stoneflies, dobsonflies, caddisflies and crustaceans were the same. Overall productivity was also the same.

Although Garnham and McMahon (1947) reported deaths among fish, other workers found fish unharmed immediately after DDT application (Cope et al. 1947, Gjullin et al. 1949, Hocking et al. 1949, Travis et al. 1951, Collins et al. 1952, Hoffmann and Drooz 1953, Corbet 1958, Hoffmann 1959). Hocking (1950) suggested that long term effects on fish may be profound.

With the exception of DDT adsorbed onto solids, different formulations show slight, if any, effect on toxicity (Fredeen, Arnason and Berck 1953, Fredeen, Arnason, Berck and Rempel 1953, Kershaw et al. 1965). Fredeen reported that only 2 out of 4 tests using DDT on solids showed any mortality among species other than blackflies. In these

2 tests, there was a reduction of mortality of 50%. Kershaw and his co-workers (1965) reported no mortality among other species. Cope and his co-workers (1949) suggested that a solution of DDT in acetone provided a safety margin between blackflies, and fish, mayflies and caddisflies.

Since the recent discovery of the phenonomen of concentration of chemical insecticides in food chains, DDT has become less popular. Its stability makes it a hazard to the environment (Carson 1962, Rudd 1964). Less dangerous insecticides are being sought. Fenthion and diazinon are potential substitutes but are not as toxic, economical or as safe to use as DDT (Jamnback 1962, Guttman et al. 1966).

2.0. MATERIALS AND METHODS

2.1. Larvae

Larvae of *Cnephia dacotensis* Dyar and Shannon, *Simulium decorum* Walker, *Simulium venustum* Say or *Simulium verecundum* Stone and Jamnback and *Simulium vittatum* Zett., were reared in the laboratory. It was not practical to separate *S. venustum* and *S. verecundum* and these two species are treated as one here; that of *S. venustum*. *C. dacotensis* was collected from one locality; *S. decorum*, from two localities; *S. venustum*, from 3 localities; *S. vittatum*, from 5 localities. Usually larvae were collected and transported back to the laboratory on vegetation and stones and then were immediately transferred to the rearing apparatus. *S. decorum* and *S. vittatum* were also reared from eggs, some after a period of refrigeration (Fredeen 1959). Larvae were usually collected during the summer with the exception of *S. virtatum* which was also collected during the fall (November) and winter (January and February).

Larvae of a number of *Prosimulium* species, mainly *P. travisi* Stone, and larvae of *Twinnia nova* Dyar and Shannon were also collected.

2.2. Rearing

Three methods were used to rear larvae in the laboratory; all of them were of a closed system. The first was similar to that of Hall and Harrod (1963) and was used during the summer of 1966. Plexiglass troughs (50 cm x 5 cm x 2 cm) were supported on a pegboard stand (1.8 m x 0.9 m) which facilitated rearrangement. The plastic reservoir contained 22 liters. Untreated well water as well as deionized water was used and was filtered through a charcoal filter (36 cm x 16 cm x 4 cm), fitted into the reservoir. The water was recirculated by a submersible pump. A temperature of 7 - 10 C was maintained by passing the water via plastic tubing through an aluminium coil submerged in a brine solution cooled by a refrigerator unit.

The second method was a modification of that used by Craig (1966). The heating unit and light were not applied but a 'Microcol' refrigerator unit was used. Temperatures ranged from 19 - 23 C. Neither of these two methods were very successful, the larvae surviving for a maximum of only 6 weeks.

The third and most successful method was similar to that used by Puri (1925) and Davies and Smith (1958). It consisted of a series of battery jars filled with from 4 to 8 liters of water. Air stones in each jar provided the necessary water movement and aeration. At the bottom of each jar there was a layer of charcoal 4 - 6 cm deep. No attempt was made to control the temperature of the water which varied with room temperature from 22 - 27 C. A mixture of deionized water and tap water was used. Blackflies were reared from eggs to adults by this method.

All larvae were fed on baker's yeast. Organic material which was gathered during collections and which accumulated in the rearing apparatus was also available to them.

2.3. Observations

Observations on live larvae were made with the use of a Wild M5 stereomicroscope through the glass wall of a containing vessel. Close study was easy with magnifications of

up to 25 times but movement was too rapid to permit detailed observations at a magnification of 50.

To slow down the rapid movements of the mouthparts, "Methocel" (Dow, Methyl Cellulose, pharmaceutical grade, viscosity 100 cps) was used to increase the viscosity of the water. Varying amounts were used. Since air bubbled into a Methocel solution promoted extensive foam, current was produced with a magnetic stirrer. The Methocel technique had varying success as larvae usually became lethargic and would detach from their substratum. No measurements of viscosity were made.

Larvae were also observed when they were attached to thin plastic or glass inverted over a container of water. Since the plastic and glass sheets were much thinner than the glass wall of the rearing jars, microscopic examination was facilitated.

Larvae were also observed in rapidly flowing water with the stereomicroscope. A small plastic bottle (10 cm x 4.5 cm x 4.5 cm) was connected to a small water pump by plastic tubing. An opening was cut along one side of the bottle. The end was also cut open and covered with "lumite" (saran gauze) to prevent the larvae from escaping. A piece of lumite was put into the bottle and the bottle was completely submerged on its side in the water. Larvae placed in the bottle attached themselves readily to the walls and to the lumite.

2.4. Morphology

Living and preserved specimens were dissected and studied. Specimens were preserved in 90% ethanol or 1 : 3 glacial acetic acid and 90% ethanol. Whole mounts of head capsules in Canada balsam were also examined. Most of the head structures could be studied without any special preparations, especially with recently moulted specimens. For detailed study, heads were treated with weak solutions of potassium hydroxide, sometimes with subsequent staining with chlorazol black. Borax carmine was used to stain muscles. Mallory's triple stain (Pantin 1960; Sharplin's modification, pers. comm.), was used to prepare head capsules for studying cuticular structures. Serial sections of heads stained in Ehrlich's haematoxylin and eosin were also studied.

Simulium vittatum, the most abundant species, was studied in detail. The other species

reared in the laboratory were studied and compared with *S. vittatum*. Larvae of *Prosimulium* species and of *Twinnia nova* were also studied.

2.5. Feeding

Ideally, a test particle used to determine the size range of particulate matter ingested by simuliid larvae should have a range of sizes, a specific gravity of 1.0, and should be spherical and non-toxic. "Sephadex" polyacrylic beads, a dextran product manufactured by Pharmacia Fine Chemicals Inc. for use in gel filtration and ion exchange chromatography, combined these characteristics better than other particles tested (pollens, charcoal, soils and various synthetic products).

All "Sephadex" beads were stained in Ehrlich's haematoxylin after being swollen. Staining did not influence the shape of the beads but the beads lost their stain after being in water several days. The beads settled slowly in still water, however, the tubulence caused by the air bubbling from air stones kept them circulating.

"Sephadex" beads of 4 types were used: "G-25 superfine", with diameters ranging from 10-40 microns; "G-25 fine", with diameters ranging from 20-80 microns; "G-100", with diameters ranging from 140-400 microns; and "G-200", with diameters ranging from 40-120 microns. Some beads from these "Sephadex" samples measured during the course of the study exceeded the diameters given by the manufacturer. This discrepancy is not surprising as the given diameters are not guaranteed. Beads with diameters ranging from 120-140 microns are not included in the size ranges as defined by the manufacturer, but were present in the swollen samples of "Sephadex".

"Sephadex" bead samples were swollen according to their individual requirements ("Sephadex" booklet No. 2, Theory and Experimental Technique). Equal volumes (17.5 ml) of each of the 4 swollen "Sephadex" types, making a total of 70 ml, were added to the rearing jars. After varying lengths of time, 10 minutes to 2 hours, larvae were removed from the jars and their guts examined. To determine the size range of beads available to the larvae, 500 randomly selected beads from each of five 70 ml samples were measured. Each of the 70 ml samples were made up of equal parts of the 4 swollen "Sephadex" types.

2.6. Estimation of Larval Age

Phelps and DeFoliart (1964) estimated the age of *S. vittatum* larvae by measuring head capsule widths and by considering the amount of differentiation of the pupal histoblasts. They defined 4 categories: "small" larvae, which have a head capsule width of less than 400 microns and no histoblasts visible to the naked eye; "medium" larvae, which have a head capsule width of 400 - 600 microns and histoblasts visible to the naked eye; "maturing" larvae, which have a head capsule width of more than 600 microns and large, white histoblasts; and "mature" larvae, which also have a head capsule width of more than 600 microns but have dark histoblasts.

For this study 3 categories: small, medium and large, were defined on the basis of the length of the cephalic apotome, the width of the head capsule at its widest part and the degree of development of the pupal histoblasts. Consideration of histoblast development was subjective. Small larvae have no histoblasts readily visible. Large larvae have coloured histoblasts or large white ones in which the pupal respiratory filaments are well differentiated. Medium larvae have histoblasts of intermediate development. The lengths and widths of the head capsules of the 4 filter feeding species studied are tabulated below (table 2). Small larvae here probably include instars 1 - 3; medium larvae, instars 3 - 5; and large larvae, instars 5 - 7. The laboratory conditions during rearing may have influenced the size of the head capsules. Further, larvae infected with parasites are larger than uninfected ones of the same age. The incidence of parasitism was greater in late summer and winter populations.

No small larvae of *S. decorum* and *S. venustum* were collected so that no measurements of small larvae of these two species were made.

Table 2. Size in microns of head capsules of small, medium and large larvae of 4 species of blackflies.

	Small		Medium		Large	
Species	length	width	length	width	length	width
C. dacotensis	140-519	120-319	520-759	320-539	760-1159	540-779
S. decorum	-599	-399	600-719	400-519	720- 919	480-559
S. venustum	-699	-699	700-799	520-599	800- 899	640-719
S. vittatum	140-499	80-379	500-819	380-659	820-1039	660-799

3.0. MORPHOLOGY

3.1. Introduction

The head capsule of blackfly larvae is subcylindrical, and tapers towards the cervical region. It is prognathous (fig. 1). Most of the cephalic structures have an array of names, many of which are confusing, or at least not helpful. The dorsal part of the head capsule has been called the clypeus (Cook 1949, Dumbleton 1964), frontoclypeus (Puri 1925) and frons (Dumbleton 1962a, b). The terminology used in this study follows closely that of Crosskey (1960), consequently the dorsal part of the head capsule is called the cephalic apotome (c. apt., fig. 1, 3). It is separated from the lateral genae (fig. 1) by a pair of cleavage lines, also called the frontoclypeal sutures (Davies 1960, Dumbleton 1964), or clypeo-frontal sutures (Cook 1949). Since the term sutures refers to any membranous areas between sclerites (Snodgrass 1935) and not necessarily to ecdysial lines, Crosskey (1960) defined these membranous areas as cephalic cleavage lines. This term is adopted here (c.c.l., fig. 1, 3). These lines are roughly parallel in well developed larvae but converge at the midline of the dorsal posterior margin of the head in first instars. The genae have also been called ocular lobes (Puri 1925) and epicranial lobes (Dumbleton 1962b, 1964).

The unsclerotized posterior part of the ventral wall of the head capsule, the area covering the subeosophageal ganglion, has been given a variety of names: epicranial cleft (Stone and Jamnback 1955), gular cleft (Sommerman 1953), postgenal sinus (Crosskey 1960), throat cleft (Dumbleton 1962a), ventral cleft (Rubtzov 1964) and ventral incision (Dumbleton 1962b, Ussova 1964). Following Crosskey's (1960) adoption of the term genae for the lateral wall of the head capsule, the term postgenal cleft is used here. The ventral plate anterior to the postgenal bridge, the union of the postgenae in the midline of the ventral wall, has been called the labial plate (Jobbins-Pomeroy 1916, Metcalf 1932), mental plate (Smart 1944), mentum (Cameron 1922), submentum (Puri 1925, Davies 1960, Dumbleton 1962a, b, Rubtzov 1964) and partly maxillary, partly labial

(Cook 1949). It has recently been considered to be part of the ventral head capsule wall and is referred to as the hypostomium (hypo., fig. 1, 3) (Grenier 1949, Crosskey 1960, Wood 1963, Dumbleton 1964, Davies 1965). Grenier considered the inner surfaces between the labio-hypopharyngeal complex and the hypostomium as the mentum and the submentum. The prementum is composed of lobes present on the anterior margin of the labio-hypopharyngeal complex (l-h., fig. 2, 43, 44). However, Matsuda (1965) describes the tendency for the submentum to become sclerotized and to fuse with the gular region of the prognathous head. The posterior margin of the submentum is then recognized by the origins of the submento-mental muscles which lie on the line connecting the posterior tentorial pits. This being the case, the ventral wall of the blackfly larval head is submental, including the hypostomium, postgenal bridge and postgenal cleft. Since most recent works have not followed Matsuda's interpretation, the areas of the ventral wall are referred to here as the hypostomium, postgenal bridge and postgenal cleft (pg. cl., fig. 2).

The occipital foramen is bordered by the postocciput (postoc., fig. 1) which is separated from the head capsule by the postoccipital sulcus. The ends of the postocciput do not meet dorsally. Two cervical sclerites (cer. scl., fig. 1) are medial to the ends of the postocciput. The posterior tentorial pits are adjacent to the postoccipital condyles at the base of the postgenal cleft.

The cephalic apotome has a number of spots, called head spots (hd. spot, figs. 1, 3), which mark the origins of the cephalic muscles. Two ocelli (oc., figs. 1, 3) are present in the centre of each gena. A pair of antenna (ant., figs. 1, 3) is present at the anterolateral corners of the cephalic apotome. In late instar larvae they are 4-segmented and bear sensory papillae on the apex of the second segment. In early instar larvae the antennae have two or three segments.

The origin of the pair of feeding organs, the cephalic fans (c. fan, figs. 1-3), located on the anterolateral corners of the cephalic apotome, is still controversial. On the basis of conflicting theories of origin, they have been considered messorial (Cook 1949), a concept

rejected by most authors as being erroneous (Snodgrass 1959, Chaudonneret 1963 a, b, and others), premandibular (Puri 1925, Fortner 1937, Grenier 1949) and labral (Crosskey 1960, Wood 1963, Davies 1965 and others). They have been termed mouthbrushes (Smart 1944, Dumbleton 1962b) and cephalic fans (Puri 1925, Crosskey 1960, Dumbleton 1962a) Since 'fan' is a more accurate description and since they are not members of the typical insect mouthparts, I prefer to call them cephalic fans.

The description of the mouthparts which follows applies to late instar larvae. Structural differences between these and younger larvae, other than numbers of bristles and spines, are mentioned. Some frequently used terms are defined below:

Bristle: A hair-like cuticular process not jointed basally. The base may be either bulbous (swollen slightly immediately above the base) or triangular (expanding to the base continuously). They may be simple (figs. 32, 33), bifid, or compound (cpd. br., figs. 32, 33, 49), having multiple apices which may be of different lengths.

Brush: A collection of bristles which may or may not be organized in a pattern.

Fan: A movable structure found only on the stem of the cephalic fan.

Microtrichium: A minute, hair-like cuticular process present on bristles or rays.

Ray: An individual component of a fan. A long, cuticular process with a flexible base.

Sensory hair: A hair-like cuticular process arising from a circular membrane (s.h., figs. 32-34, 39, 42); a tactile hair (Dethier 1963); a hair organ (Snodgrass 1935). The term 'hair' is applied only to these structures.

Spine: A short, hair-like, cuticular process with a triangular base (see bristle). Base never jointed. Spines may differ from bristles only in size, the distinction between large spines and small bristles being subjective. Spines are always simple and never bear microtrichia.

Tooth: A stout, cuticular projection from the margin of a sclerotized area; labral teeth or mandibular teeth. Base never jointed.

3.2. Structure of the Mouthparts and Related Structures

3.2.1. Cephalic Fans

3.2.1.1. Cephalic fans of *Simulium vittatum* larvae

The cephalic fans (fig. 4) of *S. vittatum* are paired structures arising from the anterolateral corners of the cephalic apotome. The stem of the cephalic fan is a blunt-ended cone. The dorsal surface is sclerotized; the ventral surface is membranous. The dorsal surface consists of two large sclerites which Puri (1925) considered segments. The larger, distal sclerite, called Pl (figs. 8, 9) by Grenier (1949), stretches from the base of the primary cephalic rays to the base of the stem. It articulates with the head capsule. Three to 6 sensory hairs are scattered over the upper third of the sclerite; one large hair is present close to the tip of the stem. The second sclerite, Pb (after Grenier 1949), is spindle-shaped and horizontally arranged. It lies basal to Pl, around the lateral side of the stem.

At each anteromedial corner of the cephalic apotome there is a knob of unpigmented and flexible cuticle (fig. 2). This is the first time it has been reported.

The ventral wall of the stem is concave. It supports 3 well developed fans (figs. 4, 5). The primary fan (p. f.) arises from the apex of the stem; the secondary fan (s. f.), elsewhere called the accessory fan (Grenier 1949) and the basal fan (Rubtzov 1964), lies basal and lateral to the primary fan; the medial fan (m. f.), elsewhere called the marginal fan (Fortner 1937, Grenier 1949) and the small fan (Rubtzov 1964), lies on the medial side of the stem.

The distal half of the ventral wall consists of two membranous lobes (fig. 5). The apices of these lobes lie between the primary and secondary fans. At its apex, the medial lobe (m. lobe) bears several small, randomly arranged spines. On its basal half the medial lobe supports the medial fan. The lateral lobe (l. lobe) also bears spines which in *S. vittatum* larvae are arranged in poorly defined rows.

The basal half of the ventral wall is reinforced by a strongly sclerotized rod, Sc1 (after Grenier 1949) (fig. 5). Some workers consider this rod to represent part of the torma (Wood 1963, Wood et al. 1963). It consists of two parts; a ventral, rectangular piece and a dorsal bar. When viewed from the side (figs. 8, 9), it resembles a 'T', the medial part forming the stem. When viewed from the ventral surface, it appears to be highly ridged as described by Grenier (1949). The dorsal part lies within the stem and articulates basally with another rod, Scb (after Grenier 1949). The apex of Sc1 extends beyond the base of the secondary fan and spreads out laterally to form a fulcrum (ext. Sc1 figs. 5, 8, 9) for the rotation of the primary fan rays. Wood (1963) called this extension the connective sclerite in larvae of *Cnephia strenua* and *Simulium pictipes*. In *S. vittatum* larvae it does not connect directly with the rays. It has neither a well defined border nor a division from Sc1. I consider it an extension of Sc1. The medial part of Sc1 extends as far as the base of the secondary fan.

The second rod Scb (fig. 5) is at right angles to Sc1, passing from articulation with Sc1 to the ventrolateral wall between the two dorsal sclerites. It forms the ventrobasal wall of the stem.

A third rod Scm (fig. 5) (after Grenier 1949) supports the medial lobe. It is the thinnest of the 3 rods. It lies almost at right angles to Sc1.

The retractor muscle of the cephalic fan inserts on the base of Sc1 and is composed of 3 bundles. Two originate on the posterior region of the cephalic apotome, the precise spot being marked externally by the posterior lateral head spots. These two bundles interdigitate with those from the other side before passing anteriorly. The third and smallest bundle originates on the midline of the cephalic apotome at the posteriomedial head spot, close to the posterior margin of the head capsule.

The rays of the primary fan are arranged in a semicircle around the apex of the stem. When fully expanded, the rays cover an angle of between 200-250 degrees. The individual

rays are sickle-shaped and hollow. Their bases are expanded into vanes of flexible membranous cuticle which stains blue after being treated with Mallory's triple stain. The rest of the base is of more rigid cuticle, and stains red (Richards 1967). The shape of the basal expansion varies with the position of the ray in the fan (figs. 6, 10-12). The rays of the lateral side of the fan have slender, narrow basal expansions; the medial rays have acute, wide basal expansions.

The primary rays have microtrichia on their concave surface. The pattern of trichiation varies within the fan and with species. The more lateral rays have fewer microtrichia. The trichiation of the primary rays of *S. vittatum* larvae begins about one-third of the length of the ray from its base. The microtrichia increase in size and frequency towards the apex. There is no pattern (fig. 13). The microtrichia are 0.4 microns long and are spaced about 0.1 to 0.05 microns apart at the apex of the ray and 1.6 to 0.05 microns apart at the centre of the ray.

The numbers of fan rays varies with instar and with species. Large larvae of *S. vittatum* have 42-54 primary rays; medium larvae, 33-51; small larvae, 28-46. First instars have 11-20 primary rays.

The bases of the secondary fan rays lie in a curved line (fig. 7). This base line connects to that of the primary rays along a row of approximately 10 blades (fig. 5). These decrease in size towards the secondary fan. These blades probably represent degenerate rays. The curve of the base line of the secondary rays contributes to the whorling of the rays during opening or closing of the secondary fan. When the fan is fully expanded, the rays cover an angle of about 270 degrees. They overlie the basal quarter of the medial primary rays. Lacking a dorsal rib, the secondary rays are weaker than the primary rays. They are curved ventrally but less so than the primary rays. The bases of the individual rays are triangular, similar to those of the primary rays, but there is less variation in the basal vanes. The entire base of the secondary rays stains red when treated with Mallory's triple stain; the ray itself does not stain.

The number of secondary rays varies from 20-40 in large larvae of *S. vittatum*;

10-30 in medium larvae; 9-16 in small larvae. First instars lack a secondary fan.

Secondary rays bear microtrichia on their ventral and lateral surfaces (fig. 17). The microtrichia are longer and denser than those of the primary rays. The microtrichia begin about one-fourth to one-third the length of the ray from its base. They vary from 1.4 to2.0microns long and are spaced about 1.0 microns apart. The microtrichia form a more acute angle with the ray than do those of the primary rays and give the ray a plumose appearance.

The rays of the medial fan differ from the rays of the other two fans in that they lie in a straight line, are not curved and have bulbous bases. The rays are parallel to each other and do not spread out when the fan is opened. The individual ray is flexible and its base is membranous, i.e. staining blue when treated with Mallory's triple stain. When both medial fans are opened, the rays reach the labrum and overlap with those of the other side.

The medial rays in the fan also vary in number. Large larvae of *S. vittatum* have 9-14 rays; medium larvae, 6-11 rays; small larvae, 4-7 rays. Medial rays of *S. vittatum* bear microtrichia (fig. 18) although the medial rays of some species do not (Fortner 1937, Ussova 1964). The microtrichia are sparse and arise from small notches only on the side of the ray. The shortest microtrichia are basal and are about 0.5 microns long. The longest are apical and range up to 6.7 microns long.

Each cephalic fan has one intermediate ray. This is located between the primary and medial fans, adjacent to the lateralmost primary ray. It resembles the medial rays in trichiation and is straight and colourless (fig. 24). The basal one-third of the ray is bare. The basal microtrichia are about 1.0 microns long; the apical microtrichia are about 6.5 microns long. The ray is present in larvae of all age groups.

The first instar of *S. vittatum* has functional cephalic fans, however, only the primary fan is present. Neither the medial nor lateral lobe is present. The primary rays have the same basal expansion found in later instars, but do not have microtrichia. The rod Sc1 is

present, bears the apodeme of the cephalic muscle and has the expanded distal tip. The fans of the second instar are fully formed. The cephalic fans of the first instar of *C. dacotensis* are similar to those of *S. vittatum* first instars. The structure of the cephalic fan of *S. pictipes* first instars, described by Wood (1963), is also very similar to these two species.

3.2.1.2. Comparison of the cephalic fans of filter feeding species of blackfly larvae.

The cephalic fans of the other species studied differ in the number of rays and in trichiation. The larvae of *C. dacotensis* also differ in that they lack small spines on the lobes of the ventral stem wall. The number of rays in each fan is tabulated below (table 3). The larvae of *S. vittatum* are included for comparison. Counts were made on 5 larvae in each group.

Table 3. Numbers of rays in the 3 fans of larvae of 4 species of blackflies.

Size	Species	Primary	Secondary	Medial
Large	*C. dacotensis*	47-56	23-35	10-15
	S. decorum	54-64	29-39	9-15
	S. venustum	34-45	12-28	8-12
	S. vittatum	42-54	20-30	9-14
Medium	*C. dacotensis*	39-50	22-32	7-12
	S. decorum	44-54	16-35	6-12
	S. venustum	41-54	20-29	9-13
	S. vittatum	42-54	11-29	6-11
Small	*S. dacotensis*	19-32	6-14	2- 8
	S. decorum	44-46	16-22	6-10
	S. venustum	18-36	10-25	5- 9
	S. vittatum	27-46	9-16	4-7

The pattern of trichiation of the primary ray of *C. dacotensis* resembles that of *S. vittatum*. The microtrichia are not arranged in a regular pattern but do occur in 2 rows along the concave surface (fig. 15). They are spaced about 0.7 to 1.0 microns apart; apically they are closer together, about 0.50 microns apart. Basally the microtrichia are shorter, 0.25 to 0.50 microns long; apically they are about 1.6 microns long. The basal one-quarter of the ray is bare. The secondary rays of *C. dacotensis* cover only the basal sixth or seventh of the primary rays. The microtrichia are about 2.5 microns long and are 0.50 to 0.70 microns apart. The rays at the edge of the fan lack microtrichia. The medial rays bear microtrichia 1.4 microns long and about 0.70 microns apart. In contrast to that of *S. vittatum*, the intermediate ray has dense trichiation. The microtrichia are 0.20 to 0.05 microns apart. They range from 0.70 to 1.15 microns long.

The primary rays of *S. decorum* have no fixed pattern of trichiation but the arrangement of one long, two short, one long microtrichium is sporadically repeated (fig. 16). The longer microtrichia are about 0.70 to 1.15 microns long; the shorter microtrichia are 0.50 microns long. The basal microtrichia tend to be shorter: 0.25 to 0.12 microns long. The interval between the long microtrichia is approximately 1.15 microns long. The basal fourth of the ray is bare. The secondary rays of *S. decorum* are sickle-shaped. The diameter of the ray increases to a maximum at the centre of the ray. The rays have many microtrichia which arise from notches as do those of the intermediate ray. The medial rays of *S. decorum* lack microtrichia. The intermediate ray bears microtrichia 1.15 to 5.0 microns long and 0.50 to 0.70 microns apart. The longer microtrichia are found at the middle of the ray. The basal one-fourth of the ray lacks microtrichia.

The trichiation of *S. venustum* primary rays is arranged in a pattern (fig. 14). Long microtrichia, 0.70 microns long, are separated by groups of 8 - 11 small microtrichia, 0.25 to 0.12 microns long. Towards the base of the ray the microtrichia become equal in length, about 0.50 to 0.70 microns long, and are 0.50 to 1.0 microns apart. The secondary rays of *S. venustum* have microtrichia ranging from 2.5 to 5.2 microns long.

They are approximately 0.50 to 1.0 microns apart. The rays of the medial fan lack microtrichia. The intermediate ray has microtrichia 1.0 to 2.0 microns long which are approximately 0.5 to 1.0 microns apart.

The dimensions of the primary fans vary between species and between larvae of different ages. The width of the open fan at its widest part and the depth of the open fan at midfan are tabulated below for the 4 species studied (table 4). The frontal area of the fan, calculated from the modified equation for the area of an ellipse:

$$F.A. = \frac{ab\pi}{4}$$

(where a = width of the fan, b = depth of the fan, $\pi = 3.14$, F.A. = frontal area), is included.

Table 4. Dimensions in microns of the expanded primary fan of 4 species of blackfly larvae at 3 stages of development.

Size	Species	Width	Depth	Area (mm^2)
Large	*C. dacotensis*	1020 - 1200	420 - 540	0.34 - 0.51
	S. decorum	800 - 1060	240 - 340	0.15 - 0.26
	S. venustum	800 - 880	260 - 420	0.16 - 0.29
	S. vittatum	890 - 1120	380 - 540	0.17 - 0.48
Medium	*C. dacotensis*	380 - 700	140 - 380	0.04 - 0.21
	S. decorum	-	-	-
	S. venustum	460 - 720	200 - 320	0.07 - 0.18
	S. vittatum	780 - 850	360 - 460	0.22 - 0.31
Small	*C. dacotensis*	260 - 340	80 - 160	0.02 - 0.04
	S. decorum	-	-	-
	S. venustum	200 - 400	80 - 200	0.01 - 0.06
	S. vittatum	460 - 560	200 - 260	0.08 - 0.12

The cephalic fans of *Prosimulium* species differ from those already described in several probably functionally insignificant aspects. Because of its taxonomic value, the arrangement of the rays of the secondary fan is important. When the fan expands, the apices of the rays lie in a straight line. This feature differentiates *Prosimulium* species, as well as some *Gigantodax* and *Cnephia* species (Wood 1963), from other genera of blackflies (Sommerman 1953). The arrangement of the bases of the secondary rays (with no curve), in addition to the length of the rays contributes to this distinction. Wood (1963) stated that the number of rays and the length of the base line of the secondary fan is a fundamental difference between the secondary fan of *Prosimulium* species and that of other species of blackflies.

The secondary fan of *Prosimulium* larvae is separated from the primary one by about 6 blades. These are of equal size. The separation between medial and primary fans is obscured by 4 to 6 large rays all of which resemble the intermediate rays. Wood (1963) represented only one such ray for *P. fontanatum*. The medial rays are bare.

The pattern of trichiation of *Prosimulium fontanatum* Syme and Davies,*Prosimulium frohnei* Sommerman, *Prosimulium fuscum* Syme and Davies,*Prosimulium multidentatum* Twinn and *Prosimulium travisi* Stone resembles that of *S. venustum*, but the pattern is more pronounced. The microtrichia point apically, not almost at right angles to the ray as in other species.

The primary rays of *P. fontanatum* (fig. 19) have long microtrichia, about 1.4 microns long, interspersed with 15 to 20 shorter microtrichia, 0.75 to 1.00 microns long. The interval between the long microtrichia ranges from 1.15 to 1.65 microns. The apices of the rays bear only 2 to 3 long microtrichia.

The primary rays of *P. frohnei* (fig. 20) have long microtrichia of 1.15 microns, interspersed with about 12 shorter microtrichia of 0.6 microns long. The interval between the long microtrichia ranges from 1.4 to 2.5 microns. Towards the apex only long microtrichia, about 2.50 microns long, are present. The most distal microtrichia are subapical.

P. fuscum (fig. 21) has primary rays bearing long microtrichia, 0.9 microns in length, interspersed with about 10 short microtrichia of 0.6 microns. The interval between the long microtrichia ranges from 0.9 to 1.0 microns. The pattern continues to the apex of the ray.

The primary rays of *P. multidentatum* Twinn (fig. 22) have long microtrichia, 1.4 to 1.6 microns long, interspersed with numerous microtrichia so fine that it is impossible to separate them individually at 1000 fold magnification. They are about 0.6 to 0.7 microns long. The interval between the long microtrichia ranges from 1.6 to 2.0 microns. The apices of the rays bear only long microtrichia some of which are as long as 2.50 microns.

The primary rays of *P. travisi* (fig. 23), have a pattern of long microtrichia, 2.75 to 3.00 microns long, interspersed with shorter microtrichia, 1.4 microns long. Like those of *P. frohnei*, the apical microtrichia are long, as much as 4.6 microns and the terminal microtrichia are subapical.

The lateral and medial lobes of the ventral wall of the stem of the cephalic fan bear numerous spines. Those of the lateral lobe of *P. travisi* larvae are long enough to cover the bases of the primary rays. The medial ventral wall of *P. frohnei* larvae also bear spines below Scm.

3.2.2. Labrum

3.2.2.1. Labrum of *Simulium vittatum* larvae

The labrum (labr., figs. 25, 26, 50) is a beak-shaped structure overhanging the cibarium (cib., fig. 50). It is joined to the cephalic apotome by an ill-defined membranous area. This membranous area (mem. ar., figs. 25, 26, 28) lacks bristles but is provided with numerous sensory hairs. In *S. vittatum* larvae the margin of the cephalic apotome immediately dorsal to the membrane has 3 patterns of pigmentation (fig. 28): a straight border, or a

border with a small indentation in the midline, or a border with a protruding central lobe.

The posterior margin of the labrum is marked by a single line of well developed simple bristles with bulbous bases (fig. 25). Behind this line there is a medial pair of large sensory hairs. Anterolateral to this line there are several triangular-based bristles. The medial area anterior to this line of bristles is bare (mem. ar.). At the anterior margin of the bare area there is another straight line of bristles which have triangular bases. The main bristled area of the labrum lies immediately anterior to this second line. The bristles occur in small groups of 2 to 4. The central ones are shorter and finer than the dorsal and ventral ones. In the midline towards the apex of the labrum there is a spindle-shaped patch of stout, blunt, conical spines (c. sp. br., fig. 25). These are located on an elevated base (fig. 48). In other species of simuliids these spines have been described as labral hooks similar to those of the thoracic proleg and the posterior disc (Hora 1930), and as pectinate hairs (Grenier 1949).

The labrum is strengthened by a spade-shaped sclerite (labr. scl., fig. 26). Some authors have considered this sclerite to consist of 3 sclerites (Puri 1925, Wood 1963, Rubtzov 1964 and others). Rubtzov stated that each sclerite bears a brush. Other workers consider the sclerite as a single unit (Davies 1965). The latter interpretation is accepted here as no sutures are evident. However, in the following description the sclerite is considered in 3 sections: the apex (ax.), the connecting rod (conn. r.) and the basal piece (b.p., fig. 27). The basal piece is at right angles to the connecting rod. The apex of the sclerite forms the ventral wall of the labral tip. The anterior margin of the apex is dentate (fig. 27). The teeth are peg-shaped, of equal length and of varying widths. In an unidentified species of blackfly larvae, 4 of these teeth, two lateral and two medial, have neural connections (D.A. Craig, pers. comm.), showing that the teeth are sensory. The teeth are covered by overhanging bristles. Behind the teeth on the dorsal surface of the sclerite the apex bears a few spines arising from small lobes. The lateral borders of the sclerite are composed of

3 to 5 sclerotized blades (l. bl.) each of which bears several bristles arranged in a row (fig. 27). The basal piece of the sclerite passes inwards and supports the epipharynx (epi., fig. 50). Its lateral edges are slightly expanded. Ventrally the connecting rod supports a lobe (v. lobe) bearing a dense brush of long, thick bristles. These are the only bristles of the labrum which are compound. Grenier (1949) considered this ventral lobe the epipharynx.

The cuticle of the labrum is flexible, staining blue when treated with Mallory's triple stain. The bristles are stiff although the shorter, central ones are more flexible than the dorsal and ventral ones. The apex of the labral sclerite is of strong, nonstaining cuticle. The membranous area immediately posterior to the labrum stains pale blue.

The labrum has only one pair of muscles, the labral retractors (labr. r. m., figs. 26, 50), which insert on the ventral surface of the labral sclerite where the apex joins the connecting rod. They originate at the anteromedian head spot in the midline of the cephalic apotome. Contraction of the labral retractors brings the labrum ventrally and orally. All but one pair of labral retractors have been lost in other nematocerous larvae (Hinton 1958a, Chaudonneret 1963). Chaudonneret stated that the elasticity of the cuticle and the pressure of the interior environment play an antagonistic role to that of the labral muscles.

The cavity of the labrum is filled by a pair of dorsal glands (d. g., fig. 50) which open directly into the cibarium.

Midway between the labrum and the stem of the cephalic fan there is a patch of 15 to 20 compound, highly pigmented bristles (fig. 26). It occurs in larvae of all ages.

3.2.2.2. Comparison of labra of filter feeding species of blackflies

The labrum of the larvae of the other 3 species studied does not differ very much from that of *S. vittatum*. The patch of compound bristles is less well pigmented in *S. decorum* and in *S. venustum* larvae. In *C. dacotensis*

larvae it consists of 25 to 30 bristles and has 30 to 50 sensory hairs dorsal and lateral to it.

The labra of the *Prosimulium* species examined are also very similar to that of *S. vittatum* larvae. *P. travisi* larvae have a few curved lateral labral teeth which are longer than the medial teeth. The medial spindle-shaped patch of stout, conical spines is less well developed in *P. fontanatum* and *P. multidentatum* larvae. It is present but more dorsal in *P. frohnei* larvae.

3.2.3. Mandibles

3.2.3.1. Mandibles of *Simulium vittatum* larvae

The mandibles of *Simulium vittatum* larvae are broadly rectangular and flattened laterally (figs. 32, 33). Their bases are thicker than their apices. They are curved medially and bear brushes on their concave surface.

The mandibular articulations have changed position from those of the primitive insect, a trend found among other Nematocera (Cook 1949). The mandibles of blackfly larvae articulate in sockets formed by heavily sclerotized X-shaped structures, the postantennal buttresses (pa.b., fig. 2). Two ventrally directed arms of each buttress provide a pivot for the base of the lateral sides of the mandible. The anterior dorsal arm of the buttress supports the base of the wall of the cephalic fan; the fourth arm passes ventral to the antenna. With its points of articulation midway along the ventral arm of the buttress, the mandible moves in a plane forming an angle of 30 to 40 degrees with the vertical plane of the longitudinal axis of the body. This angle is subsequently called the angle of articulation.

The base of the mandible is strengthened by a thick, strongly sclerotized ridge which follows a longitudinal cleft in the medioventral surface of the mandible. The apodeme of the retractor muscle inserts at the apex of this cleft. The extensor inserts directly opposite at the base of the adoral surface. Both muscles originate at the posterior margin of the postgenae. The extensor consists of 5 bundles; the retractor consists of 3 bundles.

Distally the mandibles bear 3 sets of teeth (fig. 35). There are 4 black apical teeth (a.t.). These are the longest teeth. Three of these are orientated in different directions. The fourth lies just above these 3. The inner teeth (i.t.) lie in a row immediately basal to the apical teeth. These are smaller than the black teeth and are pale. They vary considerably in number between species (figs. 35-37) and instar. The first 3 inner teeth are always longer than the rest and are also on a slightly different plane. In *S. vittatum* larvae the number of inner teeth ranges from 14 to 17. Basal to the inner teeth lie the marginal teeth (m.t.). These are less well developed than the other teeth and may be very short. The number and orientation varies with species. There are two apically directed marginal teeth in larvae of *S. vittatum*. The basal one is smaller than the apical one.

The mandible bears 8 brushes (figs. 32, 33). Six consist of simple bristles; two consist of compound bristles. The apical brush (a. br.) is made up of rows of short, fine bristles of equal length. They are arranged on small lobes and curve towards the apical teeth. The first external brush (1st ext. br.) stretches from the apex of the mandible to the middle lobe (m. lobe), midway along the concave surface. It consists of numerous, fine bristles with relatively strong bases, staining red when treated with Mallory's triple stain. The bristles extend just beyond the margin of the mandible. There are a number of very fine bristles scattered behind the bases of the brush. The second external brush (2nd. ext. br.) arises from the base of the middle lobe. It is a small brush, consisting of a few long bristles which are directed apically. The middle brush (m. br.) is located immediately basal to the external brushes. It arises from the margin of the mandible. It is fan-shaped and its bristles bear microtrichia. Basal to the middle brush there is a small basal brush (s. b. br.) consisting of fine bristles. These arise from a membranous patch on the mandible. The bristles of the middle brush overlap both the small basal and second external brushes. The inner brush (i. br.), consisting of 3 to 5 thick bristles, arises from the apex of the mandibular cleft and is apically directed.

The covering brush (cov. br.) arises distal and medial to the external lobe (ext. lobe) loeated at the apex of the mandible (fig. 38). The bristles are eompound and arise from the individual lobes. In eontrast to other eompound bristles, these branch close to their bases. Both the eovering brush and the first external brush deflect away from the mandible and so deseribe a 'V' with the apieal teeth (fig. 38). This defleetion and the curve of the bristles permit the two apical brushes to eurve over the primary retracted fan of the cephalic fan.

The large basal brush (l. b. br.) is the second brush consisting of compound bristles. Rubtzov (1964) divided this brush into two parts: large basal bristles and small basal bristles. The 10 to 15 bristles are long and straight. When the mandibles are retracted the bristles extend into the cibarium.

The mandible of *S. vittatum* has 12 to 15 sensory hairs. Five to 6 of these are scattered along the adoral surfaee. There is a pair of large sensory hairs on the apieal surfaee immediately behind the first external brush (fig. 32). One hair is slightly longer than the other. The other sensory hairs are scattered around the basal eorner of the convex side.

The dorsal and basal corner has several small spines. A large spine is present on the apex of the mandible, arising on the ventral surface just behind the inner teeth. The apical lobe also has a group of small spines.

Treatment with Mallory's triple stain reveals that the basal ridge of the mandible and the postantennal buttress are of strong, rigid cutiele. The rest of the mandible itself is stronger and less flexible than that of the rest of the head capsule. The apieal teeth are strong and rigid. The inner and marginal teeth do not stain readily, suggesting that they too are strong and rigid. However, this may be due to the difficulty of getting the stain to penetrate inside of the mandible.

The mandibles of the first instar *S. vittatum* have an almost complete set of teeth and brushes. However, there are no marginal teeth and the large basal brush is represented by only one bristle. The only anatomical differenee is the position of the pair of sensory

hairs on the apex. In first instars it arises in front of the first external brush rather than behind it as in later instars. The mandible of the second instar has a similar smaller number of component parts as does the first instar but the pair of sensory hairs is behind the first external brush.

On some *S. vittatum* larvae the bristles of the large basal brush have a globular structure which have not been described elsewhere (fig. 49). These bulbs have no distinctive structural features and are always found on the bristles at the region where they branch. Usually 2 or 3 bristles in one brush each have one bulb. On later instar larvae the bulbs are darkly coloured; on younger larvae they are pale. The bulbs turn pink and subsequently become colourless when treated with a 4% solution of potassium hydroxide but they do not dissolve. The colour returns when the larvae are returned to alcohol. I have observed the bulbs preserved in 90% ethanol, 70% ethanol after Bouin's fixative, and a mixture of glacial acetic acid and 70% ethanol. I have also observed them on specimens mounted in Canada balsam after exposure to alcohols and xylene. Larvae bearing these bulbs have been found in one population from Ontario (railway yards, Belleville) and two populations in Alberta (Johnson Lake inlet, Banff National Park; Whitemud Creek, Edmonton). The proportion of larvae of the Ontario population bearing these bulbs is tabulated below (table 5). A few larvae, perhaps 5%, of the Johnson Lake inlet collections had bulbs. One specimen of *P. travisi* collected in Alberta had a bulbous structure resembling those on the mandible of *S. vittatum* larvae. It was on a large basal bristle. Two specimens of *S. vittatum* had similar bulbs on simple labral bristles.

Table 5. Proportion of *S. vittatum* larvae from an Ontario population bearing bulbs on large basal bristles of the mandible.

Size	On both mandibles		On one mandible		No bulbs		Total	
	no.	%	no.	%	no.	%	no.	%
Large	16	45.71	4	11.43	15	42.86	35	100.00
Medium	10	28.57	4	11.43	21	60.00	35	100.00
Small	3	8.57	2	5.71	25	71.43	30	100.00
No. exam.	29	29.00	10	10.00	61	61.00	100	100.00

3.2.3.2. Comparison of mandibles of filter feeding species of blackfly larvae.

The mandibles of other species studied have no major differences. Most variation occurs in the arrangement of the marginal teeth. *S. venustum* has 2 to 3 marginal teeth and these are at right angles to the edge of the mandible. The two marginal teeth of *C. dacotensis* point either apically or basally. The basal tooth is almost the same size as the apical one. In both *S. venustum* and *C. dacotensis* small spines occur at the base of the apical and inner teeth. These intermingle with the small marginal teeth.

The rows of the small apical brush of *C. dacotensis* larvae are on ridges and approach the apical teeth. The external lobe, between the apical teeth and covering brush, is more pronounced. *C. dacotensis* and *S. venustum* larvae have more sensory hairs behind the base of the first external brush; *S. decorum* larvae have fewer. In *C. dacotensis* larvae the pair of sensory hairs is located further back from the base of the first external brush.

The large spine at the apex of the mandible in both *C. dacotensis* and *S. venustum* larvae is oddly twisted. The basal, dorsal spines on the mandible of *S. decorum* larvae are stout and arranged in rows.

To compare the size of the mandibles of the 3 age groups of the 4 species, 3 parameters were measured: (1) the distance between the apex of the covering brush and the base of the second external brush, (2) the distance between the apex of the covering brush and the base of the middle brush, (3) the distance between the apex of the covering brush and the base of the large basal brush (table 6). Measurements were made on 5 larvae in each category of each species.

The parameters of the *Prosimulium* species examined show only slight variation from those of *S. vittatum*. The marginal teeth differ in their arrangement (fig. 37). Larvae of the *Prosimulium* species examined have 8 to 14 marginal teeth, more than larvae of the other 4 species studied. The apical marginal tooth is largest, the other teeth decreasing in size towards the base of the mandible. Some marginal teeth of *P. travisi* and *P. frohnei* larvae have compound apices. Larvae of these two species also have 5 apical teeth, the extra one being adjacent to the dorsal fourth tooth.

Table 6. Distances in microns between the covering brush 'c', and the base of the second external brush 'e', the middle brush 'm', and the large basal brush 'lb' of the mandibles of 4 species of blackflies at 3 stages of development.

Size	Species	c - e	c - m	c - lb
Large	*C. dacotensis*	140 - 180	180 - 200	220 - 310
	S. decorum	150 - 180	160 - 190	220 - 280
	S. venustum	130 - 150	130 - 180	220 - 280
	S. vittatum	140 - 150	160 - 180	140 - 290
Medium	*C. dacotensis*	50 - 100	50 - 120	80 - 180
	S. decorum	-	-	-
	S. venustum	70 - 120	90 - 140	140 - 220
	S. vittatum	100 - 120	120 - 140	180 - 220
Small	*C. dacotensis*	40 - 50	50 - 60	80 - 110
	S. decorum	-	-	-
	S. venustum	40 - 60	50 - 80	90 - 130
	S. vittatum	70 - 80	80 - 100	120 - 150

The apical spine is absent from all *Prosimulium* species examined. The mandibles are more darkly coloured as is the rest of the head capsule.

3.2.4. Maxillae

3.2.4.1. Maxillae of *Simulium vittatum* larvae

The maxilla of *S. vittatum* larvae is mitten-shaped, the maxillary palp representing the thumb (figs. 39, 40). The maxilla lies ventral to the mandible and dorsolateral to the labio-hypopharyngeal complex. The palp is aboral.

The maxilla is sclerotized in 3 areas which Rubtzov (1964) considered as the cardo, lacinia and galea (figs. 39, 40). According to Cook (1949), the maxilla is reduced and consists of the stipes which is partly sclerotized and partly membranous. Although the maxilla is reduced Rubtzov's terminology is accepted here. The sclerotized areas are of relatively inflexible cuticle, staining red when treated with Mallory's triple stain. The rest of the maxillary cuticle, except the pigmented area of the palp, stains blue and is flexible.

The maxillary lobe bears 5 brushes (figs. 39, 40). The ventral adoral surface bears a diffuse brush (diff. br.) composed of fine, simple bristles. These are randomly arranged and are directed apically. The bristles on the medial border become intermingled with minute spines arranged in small rows of 3 to 5. Medial to this brush, on the apical half of the lobe, there is a middle brush (m. br.) similarly composed of fine, simple, randomly arranged bristles. These bristles are larger and directed basally. A large oral brush (l. or. br.) lies adjacent to the middle brush. This brush consists of 10 to 15 rows each containing 12 to 15 bristles. The bristles are long, thick and darkly pigmented. The basal rows are composed of larger bristles. All bristles point apically. Laterobasal to the large oral brush lies a small oral brush (s. or. br.) similarly composed of bristles arranged in rows. The fifth brush is the apical brush (a. br.), consisting of 6 to 10 simple bristles. These are long, thick and have expanded bases.

The lacinia lies basal to the large oral brush and adjacent to the small oral brush. On its distal border it bears a row of teeth which increase in size towards its apex. The most distal tooth is spine-like, long and curved at its apex. The lacinia has one small patch of bristles on the corner adjacent to the small oral brush.

The galea, on the dorsal surface, is bare with the exception of a centrally positioned, large sensory hair and 5 to 8 small apical hairs.

The maxillary lobe bears two large spines (sp.). The largest is curved, stout and often blunt. It is located between the middle and large oral brushes just below the apex of the

lobe. It has a raised base which it shares with a large sensory hair (ass. s. h.). The second spine is located between the middle and large oral brushes near the base of the lobe. On its dorsobasal side there is a patch of several short, densely arranged bristles.

Basal to the middle brush and adjacent to the small oral brush there is a bare area with a lobulate surface (lob. ar.). These small lobes are present on all specimens and have been described elsewhere (Rubtzov 1964).

The palp of the maxilla is one-segmented and slightly shorter than the lobe (figs. 39, 40). It tapers distally. It is darkly pigmented with the exception of the apex. It bears 10 to 15 sensory hairs scattered over its pigmented surface. The apex bears 4 to 6 sensory papillae. On the cardo at the adoral side of the base of the palp there is a group of 6 to 8 sensory hairs. On the ventral surface of the cardo there is a patch of 20 to 25 fine, unpigmented bristles.

The maxilla has two muscles. The retractor, consisting of 3 bundles, inserts on the middle of the oral surface level with the base of the palp. It originates near the posterior border of the postgena, and moves the maxilla dorsomedially towards the cibarium. The extensor inserts basal to the retractor at the medioventral corner of the postgena, ventral to the retractor. It moves the maxilla ventrolaterally. The palp has no muscles (Craig 1968).

The maxilla of the first instar of *S. vittatum* is fully developed. The bristles are smaller and fewer. The palp has 2 or 3 sensory hairs.

3.2.4.2. Comparison of the maxillae of filter feeding species of blackflies.

The maxillae of the larvae of the other species studied resemble that of *S. vittatum* larvae closely. In *S. decorum* larvae the bristles of the apical brush are compound. The short bristles adjacent to the second spine have a raised base. The palp is slightly longer than the maxillary lobe and bears approximately 7 sensory hairs and 4 to 6 sensory papillae at the apex. There are 5 to 8 sensory hairs at the base of the palp. The patch of bristles basal to the palp is closer to the maxillary lobe.

In *S. venustum* larvae the adoral brush is not as well developed as that of *S. vittatum*. There is an additional small patch of fine bristles basal to the maxillary lobe. It has 6 to 8 sensory hairs and 5 sensory papillae. There are 6 to 9 hairs at the base of the palp.

The sensory hairs at the base of the palp of *C. dacotensis* larvae are longer than those of the other species. There are about 10 hairs present. The palp has 8 to 10 sensory hairs and 5 to 6 sensory papillae.

Among the *Prosimulium* species examined, the structure of the maxilla is exceedingly consistent and closely resembles that of the maxilla of *S. vittatum* larvae. The basal patch of hairs is well developed, consisting of long, darkly pigmented bristles. The sensory hairs basal to the palp are very long.

3.2.5. Labio-hypopharyngeal Complex

3.2.5.1. The labio-hypopharyngeal complex of *Simulium vittatum* larvae.

The labium and the hypopharynx are considered together because they form a complex unit and because the homologies of the labium are under dispute (Crosskey 1960). The labio-hypopharyngeal complex (l-h., Figs. 2, 50) fills the ventromedial part of the mouth area. The complex is broadly semicircular and is in two main parts (figs. 43, 44). The dorsal part, called here the hypopharyngeal lobe (hy. lobe), lies directly over the ventral labial lobe (labi. lobe). Both lobes are strengthened by a complicated set of sclerites. They are covered ventrally by the hypostomium.

The labio-hypopharyngeal sclerites of *S. vittatum* larvae stain red when treated with Mallory's triple stain. The rest of the complex, with the exception of the bristles and the lobes of the liguae, stain pale blue.

The anterior margin of the hypopharyngeal lobe is a sclerotized ridge (a. hy. m.) which pass laterally to the corners of the lobe. From the corners a compound, sclerotized ridge (bars 'x' and 'y') passes dorsally to form part of the hypopharyngeal suspensorium

(hy. sus., fig. 44). The dorsal part of the suspensorium encircles the pharynx. There is a second sclerotized ring occurring slightly to the posterior. The dorsal surface of the base of the hypopharynx is strongly sclerotized (b. hy.) and marks the anterior of the cibarium. It is concave and contoured to fit the labrum. At the lateral margin of this ridge the suspensorium is connected to the ventroposterior arm of the postantennal buttress by a membranous cuticle (conn. pa. b.).

The labial lobe has a single sclerotized anterior ridge (a. l. m.). This is dorsal and subapical. Viewed dorsally, it has a medial depression in which the sensory lobes lie (fig. 43). The lateral walls of the labial lobe are formed by a thick labial sclerite (labi. scl.), the posterior part of which is connected to the posterior part of the hypopharyngeal skeleton. A basal prong 'a' passes posteriorly from the ventroanterior margin of the labial sclerite underneath the labial lobe.

The anterior margin of the hypopharyngeal lobe has two rows of bristles (fig. 45). The bristles are short and simple. The medial bristles of the dorsal, more anterior row are stout and spine-like. The medial bristles of the posterior row are compound. The lateral margins of the hypopharyngeal wall are provided with small, fine bristles. The labial margin bears one row of short bristles and one row of blunt, paired teeth (fig. 45). Grenier (1949) numbered the rows of the hypopharyngeal and labial bristles; rows 1 to 3 are hypopharyngeal and row 4 is labial. His third row of the hypopharynx is probably the medial bristles of the dorsal row. These are larger than their fellows and point dorsally rather than anteriorly.

The labial lobe lies ventral to the labial ridge and bears numerous long bristles on its apical and ventral surface (labi. br.). The dorsoapical surface bears two prominent spherical sensory lobes (sen. lobe, fig. 45). These are thin-walled and their apical surface is lobulate. The posterior wall is thicker than the other walls. The sensory lobes bear a varying number of basiconic sensilla (b. sen.). *S. vittatum* larvae have 6 to 7 on each lobe. In some species there is a trio of small structures on the medial part of each

lobe. Rubtzov (1964) referred to them as 'Hocker' (tubercles). *S. vittatum* larvae lack them.

The lobes of the ligulae (lig. lobes) are present medial to the sensory lobes (fig. 45). These are paired, slender and L-shaped. They are strongly sclerotized, and stain red when treated with Mallory's triple stain. Ventral to the lobes of the ligulae there is a small brush of short bristles (v. br., fig. 43).

According to authors who consider the ventral plate as hypostomial, the ventral surface of the labial lobe represents the mentum, and the apex of the labial lobe including the sensory lobes represents the prementum (Grenier 1949).

There are no sensory hairs of the labio-hypopharyngeal complex.

The salivary canal (sk. can.) is formed dorsally by the hypopharyngeal lobe and ventrally by the labial lobe. Its opening is a slit. The paired salivary ducts pass anteriorly along the midline of the head capsule and fuse to form the salivary, or silk, canal in the medioventral part of the head. The silk canal continues forward and expands laterally at the level of the first hypopharyngeal bar to join the corners of the labio-hypopharyngeal complex. The wall of the silk canal is reinforced by annular thickenings in its cuticular intima. The fusion of the salivary ducts begins ventrally. The dorsal surface of the canal has a dorsomedial projection formed from the dorsal walls of the ducts for some distance anteriorly (fig. 51). The silk thread emitted from the silk canal is dorsoventrally flattened and grooved along the midline. This latter feature may be a result of the dorsomedial projection of the paired character of the salivary ducts.

The labio-hypopharyngeal complex has two muscles. The paired muscles of the 'press' of the silk canal stretches from the dorsolateral surface of the hypopharynx to the midline of the roof of the silk canal. This muscle is referred to as M_3 by Grenier (1949). The second muscle, called M_2 by Grenier (1949), inserts on the posterior tip of the labial sclerite and originates at the posterior margin of the postgenae adjacent to the postgenal cleft. It pulls the labial lobe posteriorly.

A pair of ventral glands (v. gl., fig. 51), closely resembling histologically the dorsal glands, occurs at the corners of the labio-hypopharyngeal complex adjacent to the labial sclerite. They have no apparent opening.

3.2.5.2. Comparison of the labio-hypopharyngeal complex of filter feeding species of blackfly larvae.

Differences between the structure of the labio-hypopharyngeal complex of *S. vittatum* larvae and that of the larvae of other species studied are found in the sensory lobes and in the bristles of the anterior margin of the hypopharyngeal and labial lobes. In *S. decorum* larvae the bristles of the anterior margin are longer than those of *S. vittatum* larvae. Both *S. venustum* and *C. dacotensis* larvae compound bristles in the midline of the anterior labial margin. These bristles, ranging in number from 2 to 6, occur on small individual lobes and are longer than the lateral, simple bristles. In larvae of *S. venustum* the lateral bristles arise from the lobe rather than from the labial margin itself.

In *S. decorum* and *S. venustum* the number of sensory papillae on the sensory lobes range from 6 to 8. In *C. dacotensis* larvae there are 6. The trio of small tubercles (tub.) is present in all 3 species. In *S. decorum* and *C. dacotensis* they are crescent shaped (fig. 46); in *S. venustum* they are circular.

The bristles of the *Prosimulium* species examined are longer than those of *S. vittatum*. The ventral hypopharyngeal row has medial compound bristles in larvae of *P. frohnei*, *P. fuscum* and *P. travisi*. In this respect they resemble larvae of *S. venustum* and *C. dacotensis*. The compound bristles of *P. multidentatum* larvae extend along the entire margin. In all 4 species the labial brushes are lateral; they do not approach the midline. These bristles are located on small lobes. The small medial brush ventral to the sensory lobes is larger. It extends more laterally than in other species studied.

The pair of sensory lobes is present in *Prosimulium* species. In all 4 *Prosimulium* species there are 5 sensory papillae but no trio of small tubercles. None of the species

studied have paired ligular lobes. They have a group of stout, blunt spine-like bristles similar to those on the dorsum of the labrum (fig. 47). These are immediately dorsal to the medioventral brush (v. br.) and medial to the sensory lobes (sen. lobe).

3.2.6. Hypostomium

3.2.6.1. Hypostomium of *Simulium vittatum* larvae.

The hypostomium represents an extension of the ventral head capsule wall which has increased in length due to the development of the prognathous character of the head (Crosskey 1960). It is a double walled triangular plate. The margin of the inner wall is distinguished by the hypostomial fold (Wood 1963). The hypostomium is concave, forming a sheath for the labio-hypopharyngeal complex. The midline is invaginated dorsally near the apex and forms a ridge between the two sensory lobes of the labium.

The anterior margin of the hypostomium bears numerous teeth which are arranged in specific patterns (Wood et al. 1963). This arrangement has been used as a standard diagnostic character as it varies between species. The taxonomically important characters are the number of teeth, their size relative to their fellows and their simple or compound nature.

A large medial tooth is separated from the lateral teeth by intermediate teeth. These teeth are pointed dorsally. The lateral margins of the apex of the hypostomium is also dentate.

The hypostomium bears a row of sensory hairs each parallel to the lateral, dentate margins. The apical hairs are larger than the basal ones. The numbers vary with larval instar and with species. There are 2 sensory hairs in each row in small larvae of *S. vittatum*, 4 to 6 in medium larvae and 6 to 9 in large larvae. Ventral to the hypostomial fold there are a number of randomly arranged sensory hairs.

The hypostomium consists of strong cuticle. The base and sides of the hypostomium stain red when treated with Mallory's triple stain; the apex remains black.

3.2.6.2. Comparison of hypostomium of filter feeding species of blackfly larvae.

The hypostomium of larvae of other species of blackflies studied are similar to that of *S. vittatum* larvae (Wood et al. 1963). The size of the teeth and the shape of the apical margin vary with species. The number of sensory hairs varies with age of larvae and species. *S. decorum* larvae have 2 to 5 sensory hairs per row; *S. venustum* larvae have 2 to 6 sensory hairs per row; *C. dacotensis* larvae, 1 to 5 sensory hairs per row.

The medial tooth of the hypostomium of *Prosimulium* larvae is trifid, having one large central point and two lateral secondary points. On each side of the trifid tooth there is a tiny basal tooth. This medial tooth aids in distinguishing *Prosimulium* larvae from those of other genera. The intermediate teeth may be simple or compound and may be located on small individual lobes. The hypostomium of larvae of the *Prosimulium* species examined have 3 to 4 sensory hairs in each row.

3.2.7. Cibarium

The anterior margin of the cibarium (cib.) is marked by the sclerotized base of the hypopharynx. Anterior to this lies the epipharynx dorsally and the hypopharynx ventrally. The walls of the cibarium are reinforced by the hypopharyngeal suspensorium. Midway along its length, the cibarial wall thickens and becomes corrugated. There is a depression in the ventral surface (fig. 50). This region of the cibarium is provided with fine bristles which are continuous with groups of small bristles present on the epipharynx. The bristles on the wall of the ventral depression are longer than those on the dorsal surface. In the ventral midline, the bristles are stout, blunt and conical, resembling those of the spindle-shaped patch on the labrum. Both epipharyngeal and cibarial bristles are directed posteriorly.

The cibarium has two pairs of muscles. Both are dorsal dilators. The anterior pair

insertsmedially on a sclerotized disc on the dorsal wall of the cibarium in between the two rings of the hypopharyngeal suspensorium (disc, fig. 43). They originate on the dorsal part of the cephalic apotome lateral to the labral retractor, at the anterolateral head spots. The second smaller pair of muscles inserts on a smaller sclerotized disc in the midline of the dorsal wall of the cibarium posterior to that of the anterior muscles. These originate on the cephalic apotome just posterior and adjacent to the anterior pair of muscles.

3.3. Comparison with Non-filtering Simuliidae

The head capsule of the larva of *Twinnia nova* (Dyar and Shannon) is more tapered anteriorly (fig. 3) than that of the other blackfly species studied. The cephalic cleavage lines converge both anteriorly and posteriorly and the ends of the postocciput meet dorsally in the midline. The ventral wall of the head capsule is almost complete. The postgenal cleft is very shallow and the postgenal bridge is complete. The antennae are 4-segmented. Two sensory papillae are present distally on the second segment.

The labrum of the larva of *Twinnia nova* is joined to the cephalic apotome by a membranous area (mem. ar.). The anterior margin of the cephalic apotome is straight (fig. 3) rather than curved as in filtering species. The arrangement of the labral bristles differs greatly from that of other species studied. There is a well developed mediodorsal brush (d. br.) of simple bristles which are darkly coloured, blunt and curved at their apex (figs. 29, 31). They do not point in any one direction. In larvae of *T. tibblesi* Stone and Jamnback, these bristles are pectinate (Davies 1965). The base of the brush is reinforced by a sclerotized plate, termed the basal plate (b. pl) by Davies (1965). Immediately ventral to this brush there is a group of thinner, simple bristles. These are shorter than those of the dorsal brush but longer than the rest of the labral bristles. They curve ventrally. The lateral and apical areas of the labrum are covered with smaller simple bristles which occur in groups of 2 to 5. All of them are directed medially. The

ventral lobe (v. lobe) of the labrum is supported by the connecting rod (conn. r.) of the labral sclerite (labr. scl.). It bears simple bristles which are not so well developed as the compound bristles of the other species of blackflies studied.

The labral sclerite is similar to those of the larvae of other species studied. The apex (ax.) has teeth along the anterior margin. There are 10 to 12 teeth present (fig. 29). These are longer than the labral teeth of the other species. The basal piece of the labral sclerite is orientated at right angles to the connecting rod (fig. 31). It supports the ventral surface of the labrum and epipharynx.

The medial pair of sensory hairs on the dorsum of the labrum is well developed. These are immediately posterior to the dorsal brush and not on the cephalic apotome as in other species. There is a scattering of small sensory hairs on the cephalic apotome.

The dorsal gland fills the cavity of the labrum. Histologically it is the same as that found in other species but it is composed of fewer cells.

The labrum of *T. nova* larvae has two pairs of labral retractor muscles. The medial pair is homologous with the medial retractor muscle of filtering species. It inserts on the ventral surface of the labrum immediately posterior to the connecting rod of the labral sclerite and originates on the midline of the posterior half of the cephalic apotome. The lateral pair is smaller and each muscle consists of two bundles. They originate respectively, anterior and posterior to the medial labral retractor muscles. The origins of the lateral retractors are marked externally by the medial head spots. These lateral muscles pass between the two lobes of the dorsal gland and insert dorsally to the medial retractors at the lateroposterior margins of the labrum. The lateral retractors differ from those described by Davies (1965) in *Twinnia tibblesi* larvae in that they do not insert on the curved rod (c.r.) which articulates with the basal plate of the dorsal brush (see below). Furthermore, the lateral retractors of *T. tibblesi* larvae consist only of one bundle each and this originates posterior to the medial retractors.

The insertion of the lateral muscle on the curved rods in *T. tibblesi* indicates that

this muscle is homologous to the cephalic fan retractors (Davies 1965). It suggests here that the two bundles of the lateral muscles and their individual origins in *T. nova* possibly foreshadow the complex origin of the 3-bundled cephalic fan retractors.

The pair of curved labral rods present in *T. tibblesi* larvae and *Gymnopais* sp. larvae (Davies 1965) is present in *T. nova* larvae. The rods lie lateral to the basal plate and appear to articulate with it. They do not form an X-shaped complex as illustrated by Davies for *T. tibblesi* larvae (his fig. 47, 1965). The curved rods (c.r., figs. 30, 31) are immediately anterior to the bare knobs found in filtering species adjacent to the cephalic fan stem (fig. 2). They are in the position in which the cephalic fan stem sclerites occur in filtering species. Davies points out that the orientation of the rods is nearly at right angles to the cephalic fan stem sclerites. He rejects the theory that the rods are tormal, suggesting that they are homologous with the cephalic fan sclerites and that the cephalic fans are tormal. Wood (1963) homologized the curved rods, the sclerites of *Gymnopais* larvae and the cephalic fan sclerites, considering them all tormal in origin.

The mandible of *T. nova* is shorter and stouter than that of filtering species. It is approximately rectangular and is wider at the apex than the base (fig. 34). The mandible has a thickened ridge around its base. The inner cleft is wider. The angle of articulation is more parallel to the plane of the longitudinal axis of the body than it is in other species. Therefore, according to Cook's theory (Cook 1949) *T. nova* larvae are more advanced in this respect than filtering forms. The mandible articulates with the postantennal buttress. This is less well developed than it is in the other species studied, having only 3 arms, two passing on each side of the antennal base and one forming the dorsal mandibular articulation. The fourth arm is represented only by a pocket of rigid cuticle formed by the invagination and thickening of the margin of the head capsule. A projection of the medial side of the mandible articulates with this knob.

The retractor muscle of the mandible is very well developed. It is composed of 4 large bundles inserting on a large, sclerotized apodeme located on the oral surface of

the mandible. The bundles originate laterally on the posterolateral partsof the postgenae, ventral to the extensor muscle. The ventralmost bundles originate adjacent to the postgenal cleft; the dorsalmost, immediately lateral to the labral muscles. The extensor muscle consists of 4 smaller bundles which insert on a shorter, non-sclerotized apodeme on the adoral side. They originate lateral and dorsal to the retractor muscle. Both these muscles are larger than those of filtering species.

The arrangement of teeth on the mandible differs from that of the other species studied (fig. 36). There are 10 to 12 teeth arranged in a curved line along the apex. The dorsalmost teeth are largest with the size of the teeth decreasing towards the base of the mandible. There is an extra basal tooth between the fourth and fifth or the fifth and sixth tooth from the apex. All the teeth point apically. The apices of some teeth are occasionally broken off, presumably during feeding. There are two minute, apically-directed marginal teeth. At the base of the dorsal teeth there is a row of small spines. More small spines occur from the base of the fifth or sixth tooth to the base of the marginal teeth. Three apical spines are present behind these.

The brushes of the mandible are less well developed than those of filtering species (fig. 34). There are no covering, apical or second external brushes and the first external brush is shorter and composed of small bristles. In filtering species these 4 brushes comb the fans. The external lobe which separates the two apical brushes from the teeth is also lacking as is the inner brush. The bristles of the middle, small basal and large basal brushes are fewer and finer than those of the filtering species. Only some of the bristles of the large basal brush are compound. The medial lobe is present.

The mandibles have fewer sensory hairs. One large sensory hair is found at the base of the mid-dorsal line with a second smaller sensory hair about half way up the mid-dorsal line. There are 4 small sensory hairs on the lower half of the oral surface and two are present on the adoral surface. The pair of sensory hairs with a common base occurs immediately behind the base of the first external brush and both are smaller than those in other species.

The maxilla of *T. nova* larvae is similar in shape to that of the other species but the maxillary lobe is more tapered at the apex (figs. 41, 42). The arrangement of the brushes of the lobe is different. There is only one oral brush (or. br.) which has bristles arranged in rows. This is adjacent to the lacinia. The lacinia has numerous patches of very small bristles arranged in groups of 2 to 5, however it does not have the bristles in one corner as do the other species studied. It has small teeth on its distal border. Apical to the oral brush, the middle brush (m. br.) has long, orally-directed bristles. The apical brush (a. br.), found partly on the oral surface and continuing over to the adoral surface, has large bristles directed apically. Another large brush (2 a. br.) occurs ventral to the apical brush on the adoral side; this brush is not found in the filtering species studied. The bristles of the two apical brushes are thick and curved at their apices. The rest of the adoral surface is bare. There is no lobulate area as is found in filtering species.

The maxillary lobe has two spines (sp.). These are much shorter than those of the other species studied. Neither spine has a raised base; the apical spine, however, does have an associated sensory hair (ass. s. h.). On the bare adoral surface there are two sensory hairs, one apical and one basal.

Both muscles of the maxillae have two bundles and originate anterolateral to the mandibular muscles. The retractor has one bundle larger than the other. The smaller bundle originates dorsal to the larger one just below the ocelli. The extensor muscle originates on the posterior region of the postgena.

The maxillary palp is the same length as the maxillary lobe. It has 3 to 4 small sensory hairs scattered over the pigmented surface and 3 to 4 sensory papillae in the centre of the apex. There are two sensory hairs on the adoral side of the palp base. As in other species, a patch of large bristles is present at the base of the palp.

The labio-hypopharyngeal complex of *T. nova* larvae is similar to that of the other species studied, but the sclerotized framework is less well developed. The connection between the hypopharyngeal sclerite and the hypopharyngeal suspensorium is membranous.

Only one ring of the hypopharyngeal suspensorium surrounds the gut. Bars 'a' and 'b' are almost parallel to the ridges of the two lobes.

The hypopharyngeal lobe has two anterior rows of bristles and spines. The dorsal one consists of short spines rather than bristles. The medial spines are longer than the lateral ones. The ventral and posterior row extends across the entire width of the lobe. All bristles are simple but the lateral ones are short and conical. The labial margin is not so well developed as that of the other species studied. There are bristles on the dorsal surface of the lobe posterior to the margin. The labial brush is ventral and lateral but does not approach the midline as it does in other species. The ventral brush has uniform bristles of equal length and these lie in a straight line. They are distinct from those of the labial brush but not separated from them.

The two sensory lobes each bear 3 sensory papiliae but no trio of tubercles. The lobes of the ligula are paired, distinct structures similar to those of *S. vittatum* but they curve laterally at the apex.

The musculature of the labio-hypopharyngeal complex, the ventral glands and the salivary ducts are all similar to those of *S. vittatum* larvae.

The hypostomia of *T. nova* larvae have compound teeth. There are 3 sensory hairs per row and one mediobasal pair.

The cibarium of *T. nova* larvae does not differ from that of other species. Posteriorly directed bristles line the epipharynx and the cibarial walls. Two pairs of dorsal cibarial muscles are present but these are smaller than those of filtering species and do not insert on sclerotized discs.

4.0. FEEDING

4.1. Behaviour

Blackfly larvae attach themselves to the substratum, usually within 8 to 10 centimeters of the surface of the water, with their posterior circlet of hooks. They attach dorsal side down and rotate their body some 90 to 180 degrees to the left or right between the fourth and fifth segment. They are orientated with respect to the current so that the head is downstream from the abdomen and is held so that the fans face the current. Both body and head are constantly buffeted by the current. The angle between the substratum and the body is not actively maintained but varies with the current. Hocking and Pickering (1954) described the pattern of larval attachments in streams. Fortner (1937) described the feeding stance in detail.

Both primary and secondary fans catch particles. The particles are held in the middle of the primary fans. These particles may be retained there through 3 to 4 flicks (retraction and extension) of the fans. They may be swept out of the fan before the latter flicks closed. Loss of particles either from the fans or the mouthparts is frequent. One large *S. decorum* larvae caught 196 particles in 5 minutes; it ingested 142 and lost 54 (only particles larger than 40 microns were counted). Larvae do not flick their fans immediately on catching a particle yet they will do so without having caught any particles.

The pattern of flicking is irregular. A larva extends its fans for several seconds and then flicks them continually for several seconds. Duration of flicking and non-flicking periods vary greatly. Fifty counts were made of the flicking frequency of *S. vittatum* larvae (table II, appendix). During feeding bursts the fans flicked alternately. The times listed in the table include pauses during feeding bursts. The mean frequency for the 50 readings is 0.81 with a standard deviation of 0.33. The standard deviation is large, greater than one-third the mean. Therefore the mean can only be considered a rough approximation (Stanley 1963). The rate is comparable to that determined by Fortner (1937) f. an unidentified species of blackfly.

The pattern of feeding does not vary either between late instar and young larvae or between larvae with full guts and larvae with empty guts. The flicking frequency does not represent a feeding rate because a flicking fan is not always catching particles. The rate of ingestion is a more accurate estimate and is easier to determine (see section 4.3.2.). A comparison of the rates of ingestion and filtration may be considered an estimate of the ingestion efficiency of blackfly larvae. Assuming a rate of ingestion of 14.30 and 19.56 beads a minute (section 4.3.2.) and a flicking frequency of 0.81 flicks a second, large larvae of *S. vittatum* ingest one particle every third flick of each fan and medium larvae ingest one almost every other flick of each fan.

The mandibles and maxillae often handle particles passing into the cibarium but do not perform any special manipulatory movements in doing so. Some selection of particles with respect to particle size occurs during the transfer of particles from fans to mandibles. Larvae will retract fans which have trapped particles of 800 microns in diameter. This is larger than the mouth orifice. These are passed to the mandibles and maxillae but are not ingested. However, occasionally large sephadex particles with diameters slightly larger than that of the intima were found in the gut, compressed into a cylindrical shape by the walls of the gut. These particles progressed through the gut and did not appear to harm the larvae.

Larvae retain food in the cibarium until a bolus is formed and swallowed.

The primary fan of the larvae in the rearing jars frequently become entangled with floating debris, strands of silk or grass. Larvae showed a definite pattern of behaviour to rid themselves of the debris. As soon as the fans became entangled the larvae immediately stop feeding and retract their fans. If repeated retractions of the fans do not free the debris, the larvae arch their heads dorsally while expanding their fans. The debris is usually swept off in the current. If the debris still hangs on, the larvae twist their heads back and forth, sometimes scraping them on their abdomens or the substratum. The same pattern is occasionally carried out if an air bubble is caught on the fans or mouthparts, however, air bubbles are frequently ignored.

Whenever larvae are disturbed, either by knocking the jar, altering the rate of air flow or by a collision with floating debris, they immediately stop feeding and retract their fans. Feeding is resumed after a short period of time. Frequently larvae exhibit a searching behaviour after being distrubed. This consists of maintaining the body erect against the current and waving the head around. Larvae often change their site of attachment. Rarely did larvae remain in the same spot for 24 hours.

No incidents of cannibalism were observed among the laboratory populations, however, 3 fights were observed. In all fights a large larvae attacked a smaller one. Fighting consisted of the larvae bumping each other with their heads and scraping their mouthparts together. Larvae were never injured. During one fight, the larger larvae approached the smaller one and jabbed at the smaller one's lower abdomen with its mouthparts. The smaller larvae eventually moved out of reach of the larger one and resumed feeding. The larger one began to feed when it could no longer reach the smaller larva.

The first instar of *S. vittatum* filter with their cephalic fans. They are able to feed while suspended from the surface film of still water. They are very active. Some first instars had only yolk in their guts; others had small pieces of charcoal, sephadex and organic matter.

4.2. Movements of Mouthparts

4.2.1. Food Collection

Blackfly larvae gather food by filtering particulate matter from the water with their cephalic fans, and by scraping organic material off the substratum. The first mechanism is the most common. Particles caught in the cephalic fans are transferred to the cibarium when the fans are retracted and cleaned. The fans open when the pressure of body fluids in the fan stem is increased. The opening of the fans of living or preserved larvae can be achieved by squeezing the thorax or cervical region (Wood 1963). The maintenance of pressure in the fan stem may be controlled by the larvae through valves although as

yet there is no morphological evidence to suggest the presence of valves in the head.

The primary fans open with the ventral movement of the apex of Scl and the lateral movement of the ventral lobes of the cephalic fan stem. Infrequently when the fan expands the primary rays are hooked over each other. When this occurs the larvae immediately flicks the fan and the rays become unhooked. Fortner (1937) stated incorrectly that the closing mechanism of the cephalic fans prevented the rays from becoming entangled with each other. The secondary fan unfolds in a spiral movement. The medial fan moves laterally (with respect to the fan stem) with the movement of the medial lobe.

The fans are closed by the contraction of the cephalic fan retractor muscle. The fan stem sclerite Scl moves posterobasally and its apex moves dorsally. This movement is combined with the dorsal and medial (with respect to the fan stem) movement of Scm (figs. 8, 9). The apices of the ventral lobes of the stem move together. The primary fan closes in response to the downward movement of Scl as well as the increased curvature of the primary fan base due to the movement of the ventral lobes. The rays move together one after another like the struts of a venetian blind being raised. The rays of the medial side move first. As the expanded bases of the rays act as buffers (fig. 6), the closing of the fan is smooth and regular. The cross section of the closed rays of the primary fan (p.f.) is curved and the larger part of the curve is lateral to the stem (fig. 9). The secondary fan closes in a similar way.

The rays of the medial fan do not diverge from one another at any time. This fan closes when the medial lobe moves medially prior to the closing of the primary fan. The two other fans lie underneath the primary fan when the latter is retracted (figs. 5, 8, 9).

The stem of the cephalic fan moves medially and orally when the fan is retracted. The sclerites Scb and Pb act as fulcra.

The cephalic fans have two positions of retraction. The more frequently occurring is the retraction for cleaning. If the larvae are disturbed the fans are retracted further into the mouth orifice. In the latter case the mandibles and maxillae are also retracted.

The labrum, mandible and maxilla have a simple movement of retraction and extension. All 3 appendages may twitch rapidly, a motion best described as 'shivering'. The mandibles usually move simultaneously. They can move independently but only do so rarely. They are extended when the cephalic fans are retracted and they then retract to clean the closed fan. During periods of intensive feeding, the mandibles move in conjunction with the labrum and maxillae, extending and retracting at the same time. Infrequently the labrum and maxillae are retracted while the mandibles are extended.

On several occasions larvae in the laboratory caught asymmetrical particles. These were transferred to the cibarium by the mandibles and maxillae and ingested. Although no special manipulatory movements were seen, the particles entered the cibarium with their longitudinal axes parallel to that of the body. The shape of the cibarium coupled with the movements of the mouthparts and the folding of the fans appear to orientate particles.

The second form of feeding is that of scraping material off the substratum. The head is held more or less at right angles to the substratum. The mandibles act like claws, pulling material off the substratum. The maxillae are extended and act as supports against which the mandibles pull. The whole body is used, at times twisting in a complete circle to wrench material free. The labrum, mandibles and maxillae sometimes 'shiver' while the larvae feed off the substratum.

The mandibular teeth scrape the surface. The orientation of the apical teeth is suited for this function. The external lobe of the mandible prevents the apical brushes from scraping although they may collect superficial material scraped free by the mandibular teeth. The bristles of the labrum, especially those of the ventral lobe, also collect material. The labral teeth are too well covered by bristles to be useful in substratum feeding. The position of the hypostomial teeth, slightly more dorsal than the rest of the hypostomium, and their covering of sensory hairs suggests that the hypostomium is not used in scraping.

4.2.2. Combing

The transfer of particles from the fans to the cibarium occurs when the fans retract. The fans are combed by the mandibles and labrum. The inner surface of the mandible is contoured to fit the curve of the folded fan. The labrum similarly fits the curve of the labral surface of the fan (fig. 38). The folded fan passes underneath the covering and first external brushes of the mandible and above the middle lobe of the mandible. These brushes comb the convex surface of the folded fan. The second external brush of the mandible passes beneath the fan. The mandibular bristles bend backwards while they comb the fan rays. The mandibles are very active during feeding and comb the fans several times during one retraction of the fans. Both mandibles and labrum retract while the fans are extended, combing each other free of particles. When the fans are held extended for long periods the mandibles are also extended.

The fans are well adapted for filtering; the mandibles are well adapted for combing the fans. The development of the labral bristles and mandibular brushes, the shape of the labrum and mandibles as well as the development of the complex fan are major adaptations for filtering. Furthermore both labrum and mandible are also capable of scraping the substratum. However, these are not as efficient scraping appendages as those of non-filtering species. The bristles of the labrum and the plane of movement, teeth and musculature of the mandibles of *Twinnia nova* larvae are better adapted for scraping. The mandibles of *T. nova* larvae are not adapted for combing fans.

The maxillae are continually active during feeding. Their role is less well defined than that of the other mouthparts. The presence of well developed brushes suggests that they aid in transferring food into the cibarium and also in scraping. The arrangement of brushes differs between filtering species and non-filtering species yet both types of larvae have maxillae well provided with brushes. This suggests that the maxillae do not assist in filtering or combing but have a similar function in all species.

The combing of the fans is not very efficient. Particles often remain in the fan throughout

several retractions. Fans are retracted when they are empty; they are still combed.

The frequent retractions of the labrum, mandible and maxillae may contribute to the ingestion of food by pushing particles into the mouth. The ventral bristles of the labrum and the basal brushes of the mandible enter the pharynx. When the primary rays of the cephalic fan enter the pharynx, these bristles may comb the apices of the rays; they are not in the position to comb the rays outside of the cibarium. However the large basal and middle brushes may act as guides for the rays or food particles; they may keep the epipharynx and the bases of the fan stem, mandibles and maxillae free of particulate matter. The inner brush of the mandibles protects the mandibular cleft; it has no role in combing.

During feeding the proleg is held close to the body with its tip just below the hypostomial teeth. This position contributes to the streamlining of the body. The proleg is often brought close to the mouthparts to be cleaned of debris or silk. The mandibles shiver.

4.2.3. Silk Secretion

Blackfly larvae secrete silk very rapidly. Within a few seconds a larva can select a new site of attachment, produce a silk strand, apply it to the substratum and hook into it with its posterior organ of attachment. Throughout the process the fans are extended, held out of the way of the sticky secretion. The mandibles, maxillae and labio-hypopharyngeal complexare in constant and rapid motion. The labio-hypopharyngeal complex moves anteroposteriorly. The mechanism by which the silk is brought anteriorly and out of the canal is not clear. The M_3 muscle of the labio-hypopharyngeal complex dilates the silk canal. Silk may be sucked forward by the increase in diameter of the canal. The simultaneous action of the labio-hypopharyngeal complex retractors may help this movement. The labio-hypopharyngeal complex acts as a press, and the activity of the M_2 and M_3 muscles may contribute to the dorsoventral flattening of the silk strand. The constant motion of the mouthparts and the body may also aid in the anterior movement of silk.

The head is repeatedly extended and retracted; it arches upwards and stretches forwards. The proleg hooks onto the silk strand and draws it down from the silk canal. The mouthparts are then applied to the substratum and the silk, which is very sticky, adheres readily. Either the proleg or the posterior organ of attachment then hooks into the pad. The hypostomial teeth sever the strand(Wood 1963). Since the teeth do not move, the strand must be drawn across them by the movement of the labio-hypopharyngeal complex. The larva maintains its position by using the unsevered strand until it hooks on with its proleg or posterior organ of attachment.

The silk thread is very strong. Large larvae can be lifted out of water on the end of a 6 inch strand. The strand is used as a safety line by which floating larvae catch onto projections of the substratum. Larvae climb up their strands using their prolegs and mouthparts. Hora (1930) suggested that larvae use the stout bristles of the labrum to climb along the silk, however, the labral bristles of the species studied are not structurally suited for this task. It is probable that the mandibles and maxillae are used.

The pupal case is made of silk. Peterson (1956), Hinton (1958b), Burton (1966), and others have described the spinning of the cocoon. The fans are retracted and the mandibles rarely move during cocoon formation. The cocoon is spun by the pharate pupa. The cocoon is of leathery, coloured silk which may be of a different composition from that of larval silk.

Larvae move along the substratum by attaching with their posterior discs onto the silk pads they secrete. Progression resembles that of the geometrid caterpillar. The path of the larvae is never in a straight line. A large larva travels a distance ranging from 360 to 900 microns between silk pads. The pads consist of several compact loops of silk. The width of the strand varies from 1 to 10 microns midway between pads and is about 25 microns wide adjacent to the pads. The continual secretion of silk during locomotion prevents the larvae from being swept away by the current. Feeding larvae have no anchor line and rely on their posterior discs for attachment.

4.2.4. Mouthpart Movements of Non-filtering Larvae

Larvae of *Twinnia nova* were observed feeding in still and flowing water. The larvae graze the substratum. Attached by their prolegs, the larvae feed off the substratum in front and to the side of themselves. The mouthparts are very active; the labrum and maxillae retract while the mandibles extend. The labrum moves so that its dorsal brush scrapes the substratum while the mandibles move nearly parallel to the labrum, their teeth scraping the substratum. The brushes of the maxillae scrape the substratum when the maxillae are retracted and move dorsomedially with respect to the larval body. The mouthparts 'shiver' as do those of the filtering species. Periodically the larvae cease to feed and clean their mouthparts. Cleaning is achieved in the same manner as by filtering larvae, i.e. brushing the mouthparts against each other so that the mandibles clean the labrum and the maxillae and are in turn cleaned themselves.

The secretion of silk is carried out in the same way as in filtering species. Having cleaned the substratum around them of food, larvae progress forwards or sideways to a new site. Larvae appear to search for a new site by raising their heads up from the substratum and waving them around.

Larvae were observed grazing the surface of strands of algae. Larvae pick at the algae by grasping filaments between their mandibles and slowly moving their mouthparts along them. Larvae were also observed eating filaments of algae by progressively ingesting from one end along the filament.

4.3. Ingestion

4.3.1. Food

Blackfly larvae are unselective with respect to quality of their food. Gut contents of larvae collected from the field consist of leaf litter, spores, pollen, algae, pieces of plant stems and unidentifiable organic debris. Fragments of insect cuticle are the only recognizable animal matter present. These include pieces of blackfly larvae, pupal

respiratory filaments, head capsule parts and mandibles. The gut contents of larvae reared in the laboratory also had a large proportion of charcoal and, after the addition of yeast to the jars, clumps of yeast. Silt forms the bulk of the inorganic components.

The organic contents of the gut are not always digested. There is no visible difference between contents in the foregut and rectum. R.W. Dunbar (pers. comm.) observed larvae of *Prosimulium urnisum* Edwards excreting green algae apparently unaffected by their passage through the gut.

Measurements were made of 200 particles ingested by blackfly larvae collected in the field. These particles were among the largest the larvae ingested. The two largest dimensions of the particles were measured. Sizes ranged from 0.5 to 300 microns in length and 0.5 to 120 microns in width. Most particles were 20 to 100 microns long and 10 to 60 microns wide. Fragments of insect cuticle which are flexible and may have been folded during feeding were the largest particles ingested. The biggest of these were 500 x 160 x 120 microns, 440 x 120 x 40 microns, 320 x 120 x 60 microns.

The smallest gut particles measured were 0.5 microns in diameter but smaller particles were abundant. Due to the nature of the organic debris which adheres to the microtrichia of the primary rays and is transferred to the gut when the fan is cleaned, it was not possible to get accurate measurements of the smaller particles.

Diameters of particles ingested by first instars ranged from 4 to 0.5 microns and smaller. Second instars ingested particles with a maximum diameter of 8.5 microns.

The size range of sephadex beads ingested by larvae in the laboratory are tabulated below (table 7). The difference between the size distribution of beads available to the larvae and those ingested by the larvae were tested for significance using the Chi-square test. The level of significance was set at $P = 0.05$ with P being the probability. Frequencies of categories less than 5 were lumped and Yates' correction was applied.The diameters of beads listed in the first column of table 7 represent midpoints of the categories, e.g. 105 represents category 95-114; 125, 115-134.

Table 7. Numbers of sephadex beads ingested by larvae of 4 species of blackflies.

Dia- meter	Freq. of beads avail.	*C. dacotensis* large	*S. decorum* med.	*S. decorum* large	*S. decorum* tot.	*S. venustum* med.	*S. venustum* large	*S. venustum* tot.	*S. vittatum* small	*S. vittatum* med.	*S. vittatum* large	*S. vittatum* tot.
25	693	140	231	1114	1345	97	116	213	79	1766	1575	3420
45	573	141	49	330	379	29	52	81	10	824	870	1740
65	282	29	13	73	86	20	32	52	2	166	272	440
85	170	7	3	45	48	17	36	53	0	118	143	261
105	107	6	4	37	41	8	26	34	1	70	146	217
125	95	2	1	38	39	1	11	12		49	100	149
145	101	1	1	14	15	4	4	8		52	99	151
165	97	2	0	22	22	0	1	1		34	57	91
185	87	0	0	16	16	0	1	1		14	32	46
205	81	1	1	28	29	0	0	0		17	28	45
225	58			18	18	1		1		3	15	18
245	44			12	12					6	3	9
265	33			7	7					0	2	2
285	17			2	2					1	2	3
305	16			3	3					1	3	4
325	16			0	0						1	1
345	12			1	1							
365	7											
385	5											
405	2											
425												
445												
sum	2496	329	303	1760	2063	177	279	456	92	3121	3348	6561
no. larvae		2	5	5	10	1	2	3	9	20	14	43

Table 7 (cont'd.).

Dia-meter	Freq. of G-200 avail.	*C. dacotensis* small	med.	large	tot.	*S. venustum* med.	*S. vittatum* med.
25	0	0	0	0	0	0	0
45	0	1	0	1	2	2	0
65	6	0	4	8	12	3	0
85	8	2	41	84	125	7	0
105	3	3	20	42	64	2	0
125	33	6	69	197	255	22	0
145	23	7	33	91	123	6	0
165	36	4	28	123	147	14	4
185	30	1	5	28	31	14	2
205	4		15	98	105	11	2
225	8			3	3	5	2
245	24			15	15	8	
265	7			1	1	0	
285	4			3	3	2	
305	1						
325	4						
345	0						
365	4						
385	1						
405	1						
425	0						
445	1						
sum	198	24	215	694	886	96	10
no. larvae		5	19	11	38	10	2

Three *C. dacotensis* larvae and one *S. vittatum* larva which did not fit into one of the 3 defined size categories of larvae (page 29) did not affect results of the Chi-square tests. Most of the *C. dacotensis* larvae and the medium larvae of *S. venustum* and *S. vittatum* were exposed only to sephadex G-200 as that was the only type then available. No small

larvae of *S. decorum* and *S. venustum* were collected live from the field or reared so the 'total' categories between species are not comparable and no comparisons have been made. Where there is an obvious difference between distributions of ingested beads, no test was applied. For example, the ingested size distribution of small *S. vittatum* larvae was not compared to the size distribution of beads available. The results of the Chi-square tests are tabulated in the appendix (table III).

Without exception the size distribution of ingested beads differed significantly from that available to the larvae in each species in each age group.

Small and large *C. dacotensis* larvae ingested particles with an insignificantly different size distribution as did small and medium larvae, however, the size distribution of particles ingested by large and medium larvae differed significantly. All interspecific comparisons showed statistically significant differences in the size distribution of particles ingested.

The individual Chi-square values (table III) indicate that larvae, especially *S. decorum* and *S. vittatum* larvae, tended to select particles of a diameter of 25 microns. The Chi-square values for this diameter are much larger than those of other beads.

The maximum size of sephadex particle ingested by each group of larvae is tabulated below (table 8).

Table 8. Maximum diameters (in microns) ingested by 4 species of blackfly larvae at 3 stages of development.

	Size of larvae		
Species	small	medium	large
C. dacotensis	105	305	325
S. decorum	-	205	345
S. venustum	-	285	185
S. vittatum	185	205	285

The minimum size was not determined because the smallest sephadex bead was large enough to be trapped by the fans. Measurements of gut contents of larvae collected in the field included sizes of about 0.50 microns, 50 times smaller than the smallest size of sephadex bead.

The gut contents of field collected *Twinnia nova* larvae consisted mostly of diatoms. Filamentous algae, spores, plant fragments and unidentifiable organic debris comprised the remainder of the organic material. Silt, the second most common material, was the only inorganic material present.

Largest particles found in the guts of preserved (in 90% ethanol) *T. nova* larvae were plant fragments which ranged in size from 210 to 150 microns in length and 4 to 20 microns in width. Largest diatoms ranged from 170 to 124 microns long and 28 to 110 microns wide. Most particles ranged from 20 to 40 microns long and 2 to 4 microns wide.

4.3.2. Rates of Ingestion

The number of beads ingested by larvae exposed to sephadex samples for a known period of time was counted. The number of beads each larvae ingested per minute was calculated and the results are tabulated below (table 9).

Calculations based on larvae with full guts may be low since the larvae had probably voided sephadex. The wide range of rates of ingestion, from 1.13 to 31.85 beads per min, is not unexpected because the feeding behaviour of individual larvae is variable. The mean rate for the 6 large *S. vittatum* larvae is 14.38 beads/min with a standard deviation of ± 7.03. The mean rate of the 7 medium larvae is 19.56 ± 8.81 beads/min. Having standard deviations greater than one-third the value of the mean indicates that these means are not valid estimates of ingestion rates (Stanley 1963). Hence, for calculating the rates of filtration, the limits set by the standard deviations are used as rates of each group of larvae.

Table 9. Rates of ingestion of 3 species of blackfly larvae. * marks larvae which had full guts.

Species	Size of larvae	Exposure time (min)	No. of beads	Beads/min
C. dacotensis	large	10	233	23.30
	large	10	96	9.60
S. decorum	large	5	138	2.76
	large	30	209	6.97
	large	30	214	7.13
	medium	30	34	1.13
	medium*	30	955	31.83
S. vittatum	large	10	81	8.10
	large	10	239	23.90
	large	10	195	19.50
	large	10	82	8.20
	large*	30	610	20.33
	large	30	187	6.23
	medium*	10	298	29.80
	medium	30	126	4.26
	medium*	20	619	30.95
	medium*	20	319	15.95
	medium	20	482	24.10
	medium	10	133	13.30
	medium	10	185	18.50

The concentration of beads added to the rearing jars was 2297.50 ± 372.29 beads/ml. The concentration of beads to which the larvae were exposed is tabulated below (table 10). The difference in volume is due to the varying sizes of rearing jars. It also takes into account evaporation of water.

Table 10. Concentration of sephadex beads available to larvae. Concentrations set by the standard deviation of mean concentration.

Conc. of sample (beads/ml)	No. beads added (col. 1 x 70 ml)	Volume of jars (beads/ml) 6000 ml	7000 ml	8000 ml
1925.21	134764.70	22.46	19.25	16.85
2665.79	186605.30	31.10	28.66	23.33

The rates of filtration of the larvae are tabulated below (table 11). For *S. vittatum* larvae rates of ingestion set by the standard deviation of the mean are used; the largest and smallest rates for the other species are used since there were only 2 or 3 calculations for each.

Table 11. Rates of filtration in 'ml/min ' of 3 species of blackfly larvae.

	S. vittatum		*C. dacotensis*	*S. decorum*	
Conc. beads	large at	medium at	large at	large at	medium at
in water (beads/ml)	7.35 21.41 (beads/min)	10.75 28.37	9.60 23.30	2.76 7.13	1.13 31.83
16.85	0.44 - 1.27	0.64 - 1.68	0.57 - 1.38	0.16 - 0.42	0.07 - 1.83
19.25	0.38 - 1.11	0.56 - 1.47	0.50 - 1.21	0.14 - 0.37	0.06 - 1.65
22.46	0.33 - 0.95	0.48 - 1.26	0.43 - 1.37	0.12 - 0.32	0.05 - 1.42
23.33	0.32 - 0.92	0.46 - 1.22	0.41 - 1.00	0.12 - 0.30	0.05 - 1.39
28.66	0.28 - 0.80	0.40 - 1.06	0.36 - 0.87	0.10 - 0.27	0.04 - 1.19
31.10	0.24 - 0.69	0.35 - 0.91	0.31 - 0.75	0.09 - 0.23	0.04 - 1.02

These values can only be considered approximate as the rates of ingestion are variable. Insufficient is known about feeding of larvae, especially the stimuli for initiating and inhibiting feeding. Further, current conditions in the rearing jars are different from those of the natural habitat of the larvae.

5.0. DISCUSSION

5.1. Morphology

5.1.1. Head Capsule

The structure of the larval head capsules of the 4 filtering species studied are very similar. There are no anatomical differences to which variations in particle size selection can be attributed. The only major morphological differences were seen in *Twinnia nova* larvae which do not filter feed.

Measurement of the head capsules, cephalic fans and mandibles of *C. dacotensis* and *Simulium* species reveal that the head capsules of all 4 species are approximately the same size. The size of the head capsule and appendages of each species increases with the growth of the larvae. Slight differences in size are shown by *C. dacotensis* and *S. vittatum* larvae. The head capsules of larvae of these two species are larger than those of *S. decorum* and *S. venustum* larvae (table 2). The fans of both large *C. dacotensis* and *S. vittatum* larvae are bigger than those of the large larvae of the other species, however, medium and small larvae of *S. vittatum* have larger fans than similar larvae of the other species. The mandibles of large larvae of all filtering species are the same size; medium and small larvae of *S. vittatum* have larger mandibles than other larvae of the same age.

The 3 patterns of pigmentation of the anterior margin of the cephalic apotome of *S. vittatum* larvae are variations within the species. This is one of several intraspecific variations found among *S. vittatum* larvae.

5.1.2. Cephalic Fans

Because *Prosimulium* is a primitive genus of blackflies, the occurrence of 4 to 6 intermediate rays in the cephalic fan and the presence of fewer blades suggests that the cephalic fans once consisted of a single big fan which has evolved into 3 differentiated fans. The central largest fan is the principal filtering organ. However the role of the

secondary fan has given rise to speculation. Some authors consider the secondary fan to increase the filtering area of the primary fan since the secondary rays extend lateroventrally to the primary fan. Others maintain that it prevents particles from falling among the bases of the primary rays or into the ventral wall thereby hindering the closing of the fan. It does both. Particles are caught by the secondary fan and those observed were not caught lateral to the primary fan. Further the secondary rays extend distal to the bases of the primary rays; the dense trichiation prevents particles from falling among the primary fan bases.

Fortner (1937) suggested that the medial fan probably stabilizes the cephalic fan stem. Others have suggested that it guides particles into the primary fan. However, as it is located ventral and basal to the primary fan, I think that this is unlikely.

Fortner (1937) also studied the opening and closing of the cephalic fan in detail. She incorrectly reported that the medial fan does not move. She described the opening of the cephalic fan as the result of an increase of pressure exerted by the body fluids being forced into the head capsule. According to her, a basal membrane ('Basalmembran') connecting the ventral surface of the bases of the primary rays to each other and to the apex of the fan stem is everted and the rays are forced upward and outward. Closing of the fan results from the contraction of the cephalic fan muscles. (Fortner 1937). The basal membrane inverts, like the finger of a glove, and the fan closes. She claimed that the synchronous coming together of the rays is due to the rotation of Sc1 about its longitudinal axis. However, in the species studied here, there is no basal membrane as Fortner described and Sc1 does not rotate. Fortner illustrated the two lobes of the ventral stem wall but did not describe their movement.

Fortner (1937) maintained that the initial extension of the fan is maximal and is subsequently adjusted by an equilibrium between the elastic cuticle of the stem and the force of the current. This equilibrium is controlled by the muscles of the cephalic fan and the muscle of the body. According to Fortner, these muscles are very sensitive

to the force of the current and it is through this sensitivity that the larvae detect current variations. Her concept of the muscular sensitivity may be correct since no rheoreceptors (Hoar 1966) have yet been recognized in simuliids.

Fortner was also incorrect in describing the cleaning of the labral surface of the closed fan by the mandibular brushes.

There is evidence (Grenier 1949, Carlsson 1962) that anatomical differences in the cephalic fans are correlated with feeding differences, however, the varying numbers of rays of the 3 fans in the species studied here is not reflected in feeding habits. Larvae of *S. decorum* have the most rays in each of the 3 cephalic fans; *C. dacotensis* larvae have the least number of rays. The primary fan of *S. decorum* larvae has a small area; the rays are shorter and closer together. The fan thus has a finer 'mesh' than that of other species. In comparison *C. dacotensis* larvae have fewer rays, a larger fan and a larger 'mesh'. The differences in 'mesh' may be responsible for the greater preference of large *S. decorum* larvae than of *C. dacotensis* larvae for sephadex beads of 25 microns in diameter. However, the data for beads with a diameter of 45 microns and data of other species show the same relationship. The medium larvae of *S. venustum* have more rays than do the large larvae. This anomaly may be a result either of the measurement of large medium larvae or possibly because medium larvae are adapted to feed more than large larvae. Phelps and DeFoliart (1964) identified two periods of intensive feeding of *S. vittatum* larvae; the first by medium larvae and the second by final instars.

The rays of the various species studied here are structurally similar. However Grenier (1949) described some ecologically important differences in the shape and strength of primary rays of 20 species of blackflies found in France. He concluded that species living in strongly flowing water have shorter, more concave rays composed of stronger cuticle than do species living in moderate currents. He lists *S. venustum* as an intermediate species. Treatment with Mallory's triple stain showed that the rays are strengthened by their dorsal rib and the ventral expansions are flexible. Unfortunately preservatives influence the hardness of cuticle and interspecific comparisons of the cuticle are not possible.

As Grenier considered the strength of the cuticle without any special techniques, his conclusions are subjective.

The microtrichia of the primary fan rays have attracted much interest. Strickland (1911) claimed that the microtrichia of each primary ray extended to the adjacent ray so that a complete sieve was formed when the primary rays were extended. Fortner (1937) suggested that the microtrichia of the secondary rays have a similar function. Both workers were mistaken. The microtrichia are rarely longer than 1 micron and the rays are about 50 microns apart at their apices. Further the microtrichia are on the concave surface of the ray and not on the side. The microtrichia of any one ray may extend to the adjacent ray but only along the basal quarter of the ray. The expanded secondary ray and their microtrichia do not form an 'abgedichteteFläche' (impervious area) as Fortner suggested.

Specific differences in the trichiation of the primary rays have no effect on feeding. Rubtzov (1964) claimed that the microtrichia on the primary rays of bloodsucking species are sparse, being 10 to 20 microns apart, and that the microtrichia on the primary rays of non-bloodsucking species are dense, being about 1 micron apart. Yet the 3 *Simulium* species, *P. fuscum, P. fontanatum* and probably *P. multidentatum* are bloodsucking species and these have microtrichia spaced about 1 micron apart or less. *C. dacotensis* is autogenous; the microtrichia are less than 1 micron apart. Thus these species do not support Rubtzov's claim.

Carlsson (1962) reported another ecologically important feature of the structure of the cephalic fans. Larvae of *P. urnisum* Edwards have 24 to 26 large rays and "relatively long 'finer' rays". They are unable to catch bacteria whereas larvae of *Wilhemia equina* L. have about 46 large rays and "relatively smaller 'finer' rays" which are probably fine enough to catch bacteria. *W. equina* is found in bacteria-rich streams; *P. urnisum* is found

in bacteria-poor streams. It is not clear whether Carlsson referred to primary microtrichia or secondary rays as 'finer' rays. Thus cephalic fans have some ecologically important structural variations, however, none are apparent among the species studied here. This is probably due to the similarity of their ecological requirements; the 3 simuliid species are all found in the same microhabitat.

The microtrichia of the medial rays of *C. dacotensis* larvae are unique among the species studied. It is doubtful that the fan acts as a filter; certainly the sparse microtrichia would be of little help if it did. Although the microtrichia on the primary and secondary rays collect fine particulate debris, the trichiation of the medial ray is probably of little functional importance.

5.1.3. Labrum

The labrum of *Twinnia nova* larvae differs from that of filtering species in that the differentiated labral bristles and their arrangement are adapted for a grazing habit. The dorsal brush of *T. nova* larvae may be represented in filtering species by the spindle-shaped patch of spines; in *P. frohnei* larvae this is located posteriorly on the surface of the labrum. The presence of the well developed ventral lobe of the labrum in both grazing and filtering species supports the scraping role of the ventral lobe bristles.

The labral sclerite of *T. nova* larvae differs from that of filtering species in orientation of the basal section. In *T. nova* larvae, the orientation probably increases the strength of the labrum to overcome resistance when the larvae graze. The apex of the labral sclerite lacks the lateral blades found in filtering species; this may also be a result of the grazing habit. The labral teeth in *T. nova* larvae are used in scraping; unlike the labral sclerite of filter feeding species, the apex of the sclerite projects out from the surface of the labrum (fig. 31). The sensory labral teeth of filtering species may be represented in *T. nova* larvae by the 4 medial teeth, or, alternatively, they may have been lost.

5.1.4. Mandibles

The mandibles of filtering larvae and of *T. nova* larvae represent two forms which are adapted to two modes of feeding. Blackfly larvae which are not typical filterers or grazers, as *Simulium oviceps* Edwards and *Crozetia crozetensis* (Wormersley) larvae, have mandibles intermediate between the two forms. In *T. nova*, the more parallel plane of movement, the arrangement of the apical teeth and the stronger development of the flexor muscle are all requirements for scraping. The more parallel plane of movement dispenses with the need for a strong mandibular articulation; the postantennal buttress of *T. nova* larvae is weaker than that of filtering species.

The variation of the arrangement of the mandibular teeth of filtering species has little functional significance. The larger number of inner teeth in *Prosimulium* larvae may be a primitive feature. The 10 to 12 teeth of *T. nova* larvae probably represent undifferentiated apical and inner teeth although their position on the apex of the mandible differs slightly from that of filtering species.

In *T. nova* larvae, the brushes which comb the retracted fans of filtering larvae are either lacking or are very poorly developed. Other species without fully developed cephalic fans have similar reduced complements of brushes. Dumbleton's (1962a) illustrations of the mandible of the larvae of *S. oviceps* and *C. crozetensis* show that they also lack apical brushes and have only poorly developed middle brushes. Davies' (1960) illustrations of the mandible of the first instar of a *Prosimulium* species shows a lack of apical brushes. The teeth of the first instar of *Prosimulium* sp. are arranged like those of *T. nova* larvae. The basal brushes in all species are the most well developed of mandibular brushes, supporting the suggestion that they aid in the passage of food into the cibarium.

The bulbs found on the large basal bristles of the mandible of some *S. vittatum* larvae are not a fungus (H.T. Brodie, Department of Botany, University of Alberta, pers. comm.) neither are they a particle impaled by the bristles. They may be some swelling of the apices of the bristles or are some type of sensory organ.

5.1.5. Maxillae

The shape and arrangement of the brushes of the maxillary lobe of *T. nova* larvae are suited for scraping. The palp of *T. nova* larvae is similar to that of filtering larvae; the maxillary lobe and the palp of filtering larvae are all similar. The apical bristles of the maxillary lobe of *T. nova* larvae closely resemble those of the dorsal brush of the labrum which also scrapes the substratum. The role of the curved maxillary spines is unknown. Fortner (1937) suggested that they guide the silk thread. However this role would be as important in *T. nova* larvae as in larvae of filtering species and *T. nova* larvae only have very short spines. They are not in a suitable position to act as guides for the retracted fans. Work under progress indicates that the apical spine in *Simulium* sp. larvae is sensory (D.A. Craig, pers. comm.).

5.1.6. Labio-hypopharyngeal Complex

The labio-hypopharyngeal complex shows no particular modifications for filtering or grazing. Differences are apparently only of phylogenetic importance. The labial brush probably keeps the silk thread clean and protects the sensory lobes. The role of the lobes of the ligulae is unknown. Because the *Prosimulium* species examined do not have paired ligular lobes but a group of conical, spine-like bristles and the *Prosimulium* secrete silk as do other species, it is doubtful that the ligular lobes are functional in the secretion of silk.

5.1.7. Cibarium

The thickening of the cibarial wall midway along its length probably aids the formation of a bolus prior to swallowing. Fortner (1937) described the movement of food through the pharynx resulting from the contraction of the pharynx. Contraction of the circular muscles of the pharynx may contribute to the passage of food in conjunction with the action of the anterior pharyngeal dilators, the cibarial dilators and the labral and mandibular bristles.

5.1.8. Glands

The function of the dorsal and ventral glands is unknown. Neither Puri (1925) nor Grenier (1949) were able to identify any secretion in the lumen of the glands. Strickland (1911) claimed that the dorsal gland secreted a sticky secretion which adhered to the epipharyngeal microtrichia and aided in cleaning the cephalic fan rays. Grenier (1949) suggested that the dorsal gland aided in digestion. He further suggested that the ventral gland is the site of formation of a specialized elastic cuticle required for the movement of the labial lobe within the sheath of the hypostomium. He supported his argument mentioning the occurrence of two similar glandular formations, one at the posterior discs of simuliids and the other at the posterior suckers of blepharocerids. More work is required before the function of the glands is clarified.

5.2. Feeding

5.2.1. Size of Food

Filter feeding blackfly larvae ingest any particulate matter of suitable size. Although the quantity and quality of food, the quantity of inorganic matter present in the watercourse and other environmental factors influence colonization by various species of blackflies, several species of blackflies may be present in the same stream community as long as there is plenty of food available (Carlsson 1962). The maximum dimension of measured particulate matter ingested by simuliid larvae ranges from 0.5 to 20,000 microns. The largest particle size is far greater than the dimensions of the cibarium therefore the larvae must be capable of ingesting long filaments of food by drawing food through the mouth continuously. The maximum size of globular natural food ingested is approximately 300 microns in diameter. The largest sephadex bead ingested was 345 microns in diameter; the largest size available was 445 microns in diameter. The majority of particles measured, both natural and sephadex, were from 10 to 100 microns in diameter. The size of particles measured by Williams et al. (1961) (table 1) and the estimates given in table I of the appendix correspond closely to those ingested by species studied here. The quality of the food is also similar.

T. nova larvae ingest smaller particles; this is probably due to the food available rather than the limitations of their mouthparts. The quantity and variety of food available to grazing larvae is limited compared to that of filtering larvae.

The sephadex ingestion experiment shows that the filtering larvae select their food only with respect to size. Chemical, nutritional and physical features other than size have no bearing on the potential of particulate matter for ingestion. This character of simuliid feeding is due to the passive nature of blackfly filtering. Although certain age groups of some species, large *S. decorum* and large and medium *S. vittatum* larvae, ingested a large number of small beads, no trend towards ingestion of any particular size is apparent. Differences in ingestion between age groups within each species is due to the increase in size of the larvae with age. Differences in ingestion between species cannot be explained by structural features.

The largest diameter of sephadex bead ingested by large *S. venustum* larvae is 185 microns; by medium *S. venustum* larvae, 285 microns. This discrepancy between the size of ingested bead and the size of the larvae may be a result of feeding habits varying with age. As previously mentioned, Phelps and DeFoliart (1964) described two periods of intensive feeding for *S. vittatum* larvae. Medium *S. venustum* larvae have more primary rays than do large *S. venustum* larvae. However, *S. vittatum* larvae have no structural evidence for periodic feeding.

Filter feeding mosquito larvae ingest particulate matter varying from 7.5 to 165.0 microns (Pucat 1962). Sizes of particles ingested most commonly by *Aedes fitchii* (F. and Y.) and *Culiseta inornata* (Will.) ranged from 15 to 22 microns. *Anopheles messae* Falleroni larvae ingest particles ranging from 22.8 to 34.2 microns in the first instar to 68 to 165 microns in the fourth instar. The diameter of ingested particles is 20% of the width of the head of the first instar and this percentage increases to 31.2% for fourth instar larvae.

Work done on chironomid larvae indicates that they ingest smaller particles. *Chironomus plumosus* L. traps all particles above 17 microns and most above 12 microns in its net (Walshe 1947). The mesh of the net of *Glyptotendipes glaucus* Mg. ranges from 5 to 40 microns (Burtt 1940). Other measurements available for filtering insect larvae are those for trichopterans. Meshes of nets range from 3 by 19 microns in *Macronema* (Sattler and Kracht 1963) to 50 to 100 microns in diameter for *Hydropsyche* (Kaiser 1962).

5.2.2. Mode of Feeding

Filtering is the principal way of feeding for simuliid species having cephalic fans. Although filter feeding larvae were observed scraping the substratum, they did so only in areas surrounding their posterior discs. When there is sufficient particulate food present in the water, scraping apparently serves only to keep the substratum adjacent to the larvae and the silk pad on which they attach free of debris. Filter feeders do not scrape as rapidly or methodically as *T. nova* larvae. Larvae are not in one site for long enough for the growth of bacteria or degeneration of the silk pad to occur. However the pad might attract micro-organisms which irritate the larvae or provide additional food.

Rubtzov (1964) stated that *Twinnia* larvae filter with their labial [illegible] brushes as well as graze, however, *T. nova* larvae were only observed to graze off mats of algae and large clumps of debris as well as the substratum. The filter feeding larvae with rays of the fans cut continue normal feeding movements of the mouthparts and particles caught on the labral bristles are transferred to the mouth (Fortner 1937). *S. oviceps* and *C. crozetensis* larvae filter with abnormal fans as well as graze (Davies 1962a). These two species probably ingest a size distribution of particles different from typical filtering species.

Blackflies are not cannibalistic. Simuliid cuticle frequently present in the gut is the remains of dead insects or exuvia filtered from the water. Fighting between larvae is not predatory but competition for sites of attachment. A blackfly larva is capable of escaping from a fellow larva before it suffers any lethal wounds. It is possible that floating first instars are caught and ingested by late instar larvae, however, there have been no observations or reports to confirm this.

5.2.3. Rate of Feeding

The rates of ingestion and filtration both depend on the flicking frequency of the blackfly larvae. Calculation of the rate of ingestion is bydirect measurement. The filtration rate is based on the concentration of particles present in the water and is therefore less reliable. Filtration rates of other species have been determined, however, these are usually based on unit weight of the animal rather than individual animals. The only rate available for another insect larva is that reported by Senior-White in 1928 (*in* Bates 1949). He reported third and fourth stage mosquito larvae of various species filtering 0.5 to 2.0 litres a day (0.35 to 1.37 ml/min). These rates are comparable to those determined for simuliid larvae (table 11), 0.04 to 1.89 ml/min. It must be remembered that simuliid larvae do not feed continuously.

The flicking frequency of a filtering blackfly species was also measured by Fortner (1937). She gives a flicking rate of 15 to 17 flicks/min for one cephalic fan of larvae in still water and 60 to 72 flicks/min for larvae in flowing water. Considering her description of the fan rays and their trichiation, the species she observed is probably a *Prosimulium* species. These rates (0.25 to 0.30 flicks/sec; 1.00 to 1.20 flicks/sec) are similar to the ones measured here, ranging from 0.09 to 1.55 flicks/sec.

The flicking frequency as well as other behaviour is influenced by current. Current tolerance varies for different species. However, larvae in the extremes of their current tolerance exhibit abnormal behaviour (Fortner 1937, Grenier 1949, Carlsson 1962 and others). The pauses between bursts of flicking are longer if the current is slower or if the concentration of food in the water is low (Fortner 1937).

Concentration of food available is a second factor influencing the rate of flicking. When the concentration of food is high the fans are more active (Fortner 1937). This suggests that the larvae can detect loading of the fans, possibly through increased resistance to the current. This is apparent among chironomids although the concentration of food has little effect on the rate of irrigation of the tubes (Burtt 1940, Walshe 1951). However, the fans of blackflies retract when they are empty. Perhaps some other mechanism,

such as the rate of swallowing, influences the rate of flicking.

5.2.4. Filter Feeding.

Jørgensen (1966) lists 3 factors on which filter feeding depends: (1) concentration of food available, (2) water flow through the filters whether this is passive as for stream fauna or created by the animal itself, and (3) the efficiency of the filter. Size of particles is a fourth critical factor. Blackfly larvae are typical filterers. This is shown by the influence of current on their feeding, the efficiency (incomplete) of their cephalic fans as filters and their selection of particles by size. Concentration of food possibly determines whether or not the larvae scrape the substratum to supplement their filtering. There is a minimum concentration of food below which the larvae cannot survive. This level is lower than that required for growth (Carlsson 1962). Even at the concentration of sephadex present in the rearing jars, sufficient for some larvae to fill their guts within 30 minutes, larvae were only ingesting one particle for every 2 or 3 flicks. This seems to be a great expenditure of energy for little reward, especially if the particle is not nutritious.

On the other hand, larvae ingest more than they require. Gut contents apparently undergo little change as they progress through the alimentary canal. In many cases this may be due to high inorganic content. This superfluous feeding reflects the automaticity of filter feeding. In addition, the fact that blackfly larvae catch particles far larger than their mouth orifice is a consequence of automatic feeding. Similarly, larvae living in streams with large amounts of inorganic material, for example glacial silt in mountain streams, may starve with their guts full of silt.

6.0. CONCLUSION

Species of filter feeding blackfly larvae ingest different distributionsof particle sizes. These distributions overlap. There is no structural variation which can explain the differences in ingestion habits. All species ingest particles within a suitable size distribution whether they may be food or not. Interspecific differences in feeding are due to differences in

behaviour. More work is required before the feeding habits of blackflies can be fully understood.

Feeding differences between filterers and grazers are parallelled by structural variations. The labrum, mandibles and maxillae of *Twinnia nova* larvae are anatomically adapted for grazing; the movements of these mouthparts are almost the same as those of the mouthparts of filtering species. The cephalic fans, labrum and mandibles of filtering species are suited for catching and ingesting particles carried by the current.

Blackfly larvae ingest larger particles than other filtering insect larvae. Since filters of insect larvae tend to have a high porosity, especially when compared to those of marine invertebrates (Jørgensen 1966), blackfly larvae probably ingest larger particles than most filter feeding invertebrates. Jørgensen suggests that *Simulium* larvae ingest smaller particles; his assumption is based on the fact that blackfly larvae are reared on diets consisting only of bacteria (Fredeen 1960). This diet is not typical for most blackfly larvae.

The automatic nature of filter feeding by blackfly larvae is a valuable means for attack and one which should be utilized. Particulate larvicides such as an insecticide adsorbed onto solids which form a suspension when added to streams are the most specific insecticides against blackflies. Grazing species, which do not filter feed and ingest smaller particles in their natural habitat than do filter feeding species, are not pests. The fact that they probably would be unaffected by such an insecticide would not detract from its value.

On the basis of this work, I suggest that particles in the larger half of the ingested size distribution, 100 to 250 microns for example, treated with an insecticide, would have a wide safety margin between toxicities for blackfly larvae and other of the stream fauna. This size range is probably suitable for most species of blackflies.

Young simuliid instars would not be affected. However, if smaller particles are administered, other species of the stream fauna would be killed. It must be mentioned that not enough members of the stream fauna have been studied with respect to size of their food. Since young instars would not be exposed, repeated applications of the insecticide would be necessary. In areas where the terrain is rough or the streams are relatively inaccessible, it

may be desirable to use a particle size distribution of 25 to 250 microns in order to minimize the need for repeated applications.

Due to the nature of the larval habitat, the exposure time of the larvae to the insecticide can only be a matter of hours at the most. Because of this and because feeding by blackfly larvae is influenced by the concentration of food and current and because larvae tend to prefer particles smaller than 100 microns, enough particulate matter would be required to 'force' the larvae to ingest it by its abundance.

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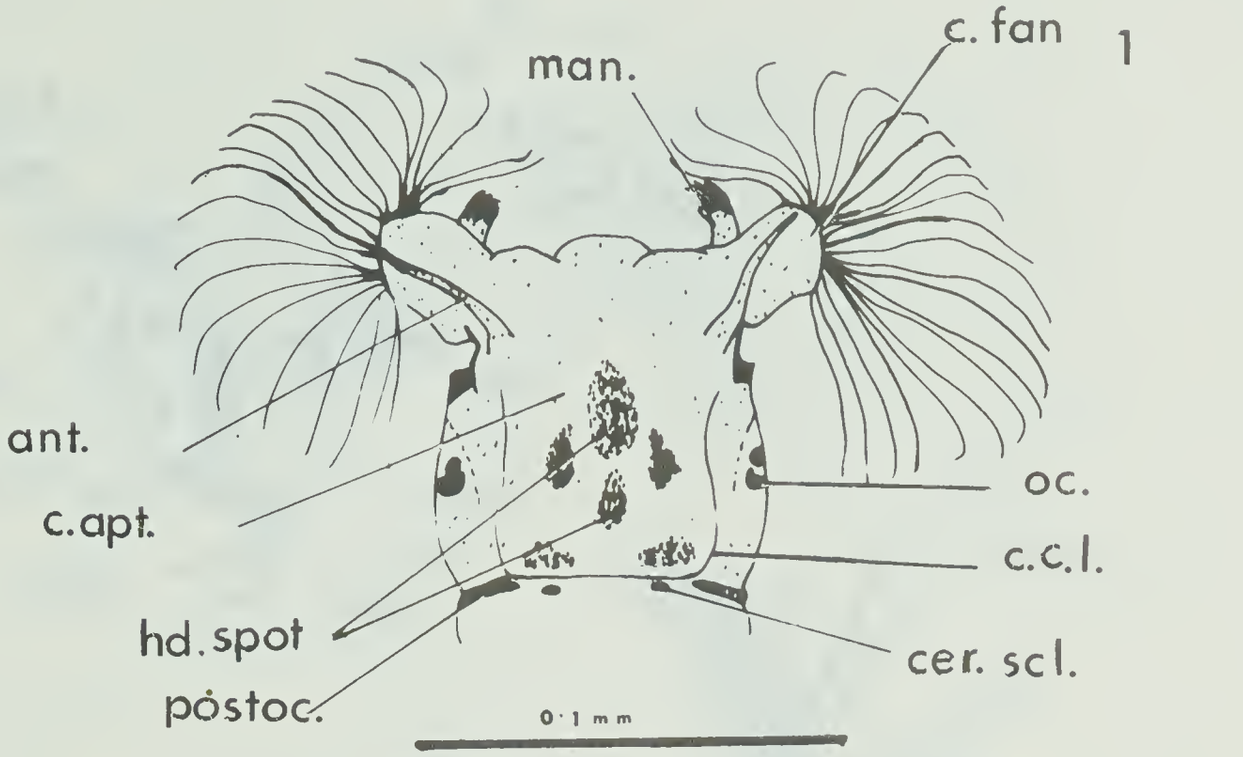
Abbreviations used in Labelling:

a	= bar 'a'	c. f. st.	= cephalic fan stem
a. br.	= apical brush	cib.	= cibarium
2 ap. br.	= additional apical brush	cib. r. m.	= cibarial retractor muscle
a. hy. m.	= anterior hypopharyngeal margin	conn. pa. b.	= connection to postantennal buttress
		conn. r.	= connecting rod
a. l. m.	= anterior labial margin	cov. br.	= covering brush
ant.	= antenna	cpd. br.	= compound bristle
apo.	= apodeme	c. r.	= curved rod
a. sp.	= apical spine	c. sp. br.	= conical spine-like bristle
ass. s. h.	= associated sensory hair	d. br.	= dorsal brush
a. t.	= apical teeth	diff. br.	= diffuse brush
ax.	= apex	d. gl.	= dorsal gland
b. ant.	= base of antenna	d. prj.	= dorsal projection
b.	= bar 'b'	d. rib	= dorsal rib
b. exp.	= basal expansion	1 ext. br.	= first external brush
b. hy.	= base of hypopharynx	2 ext. br.	= second external brush
bl.	= blade	ext. lobe	= external lobe
b. m. f.	= base of medial fan	ext. Scl	= extension of Scl
b. p.	= basal piece	f. g.	= frontal ganglion
b. p. f.	= base of primary fan	gal.	= galea
b. pl.	= basal plate	hd. spot	= head spots
b. sen.	= basiconic sensilla	hy. lobe	= hypopharyngeal lobe
b. s. f.	= base of secondary fan	hy. scl.	= hypopharyngeal sclerite
c. apt.	= cephalic apotome	hy. sus.	= hypopharyngeal suspensorium
c. c. l.	= cephalic cleavage lines	hypo.	= hypostomium
cer. scl.	= cervical sclerite	i. br.	= inner brush
c. fan	= cephalic fan	i. t.	= inner teeth

l.	= lateral
labi. br.	= labial brush
labi. lobe	= labial lobe
labi. scl.	= labial sclerite
labr.	= labrum
labr. r. m.	= labral retractor muscle
labr. scl.	= labral sclerite
lac.	= lacinia
l. bl.	= lateral blades
l. b. br.	= large basal brush
l-h.	= labio-hypopharyngeal complex
lig. lobe	= lobes of the ligula
l. lobe	= lateral lobe
l. or. br.	= large oral brush
lob. ar.	= lobulate area
M_2	= hypopharyngeal muscle
M_3	= labial retractor muscle
man.	= mandible
max.	= maxilla
mem. ar.	= membranous area
m. br.	= middle brush
m. f.	= medial fan
m. lobe	= median lobe
m. t.	= marginal teeth
oc.	= ocelli
or. br.	= oral brush
pa. b.	= postantennal buttress
Pb	= sclerite of the cephalic fan wall
p. f.	= primary fan
pg.	= postgena
pg. cl.	= postgenal cleft
ph.	= pharynx
Pl	= sclerite of the cephalic fan wall
postoc.	= postocciput
s. b. br.	= small basal brush
Sc	= sclerite of the cephalic fan
Scb	= sclerite of the cephalic fan
scl. disc	= sclerotized disc
Scm	= sclerite of the cephalic fan
sen. lobe	= sensory lobe
s. f.	= secondary fan
s. h.	= sensory hair
s. h. pr.	= pair of sensory hairs
sk. can.	= silk canal
s. or. br.	= small oral brush
s. pap.	= sensory papilla
sp.	= spine
tub.	= tubercles
v. br.	= ventral brush
v. gl.	= ventral gland
v. lobe	= ventral lobe
x	= bar 'x'
y	= bar 'y'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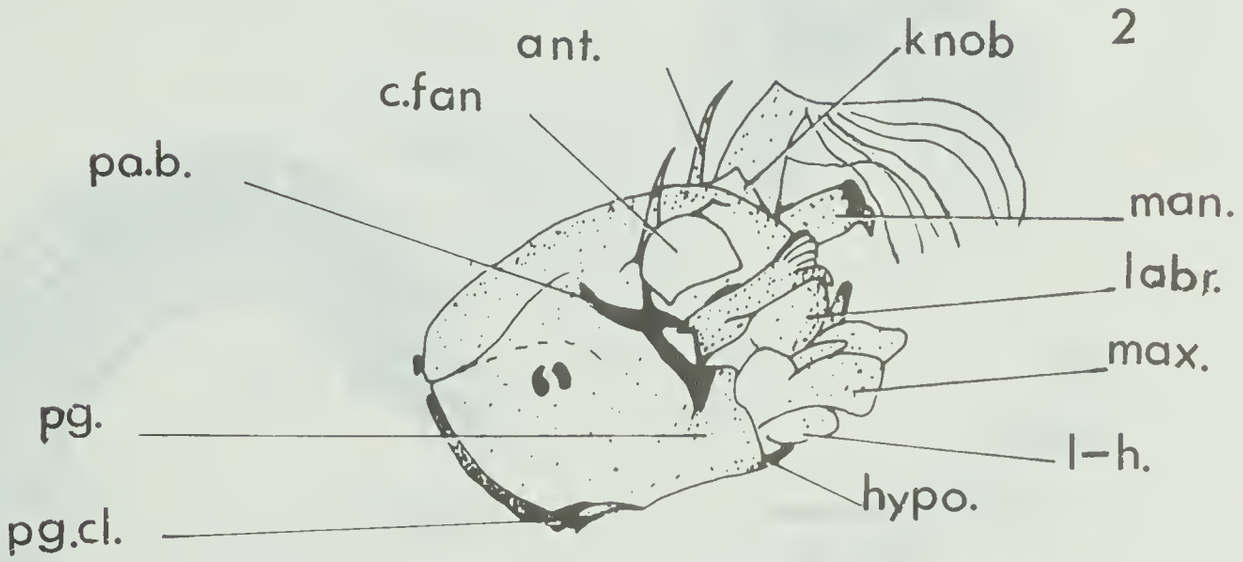
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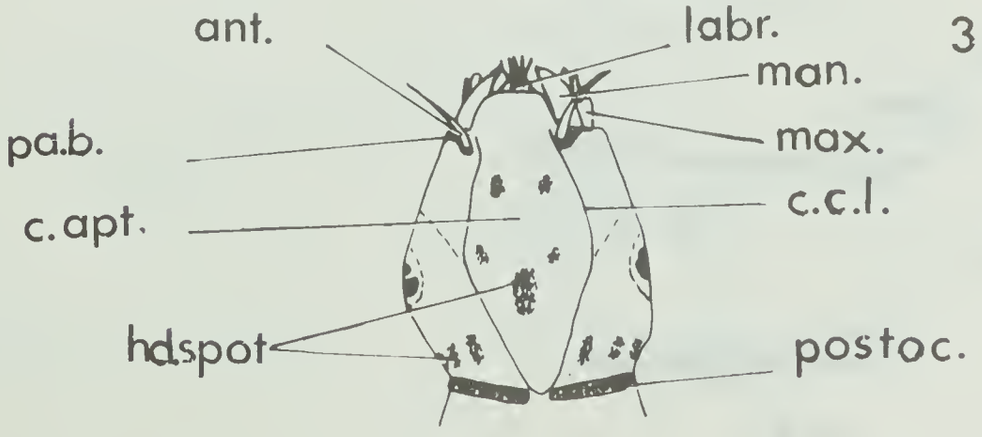
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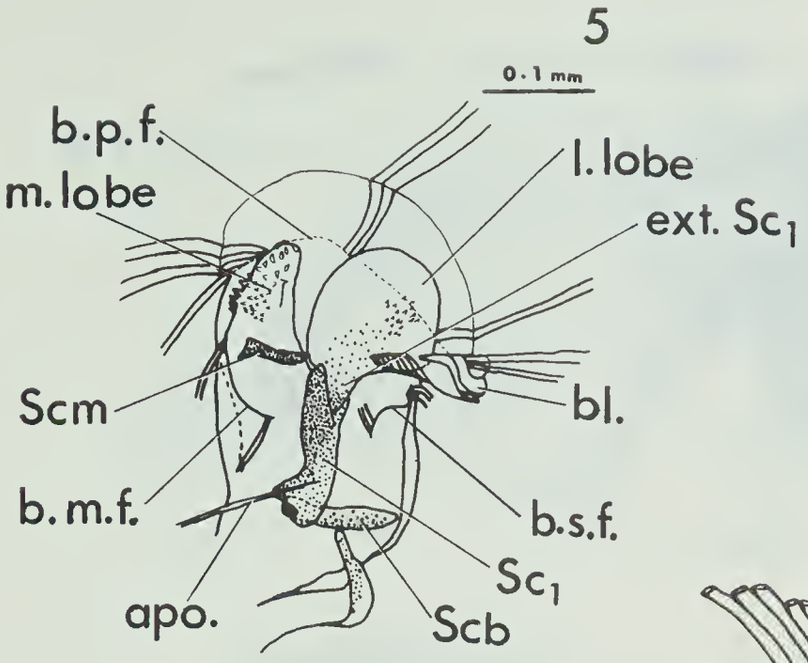
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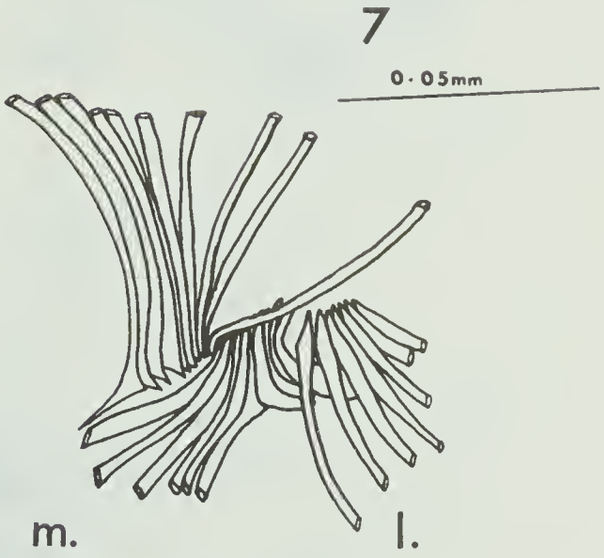
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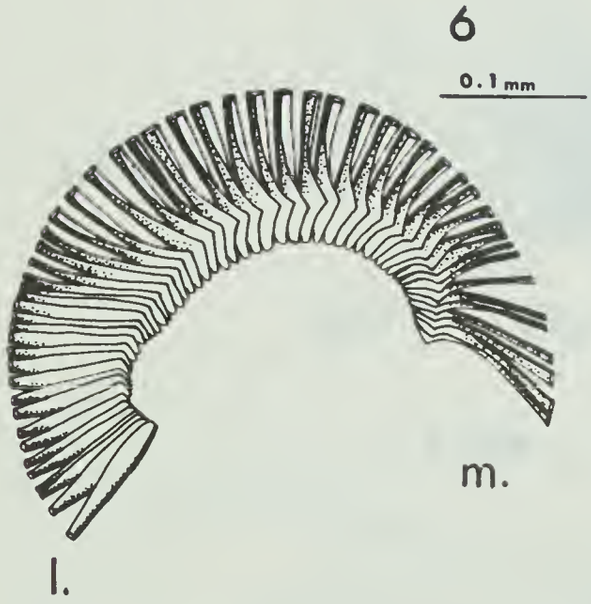
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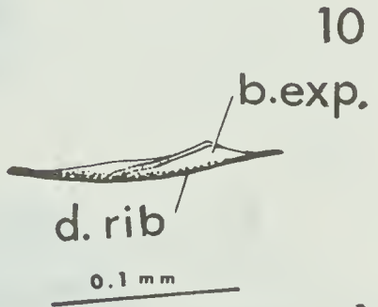
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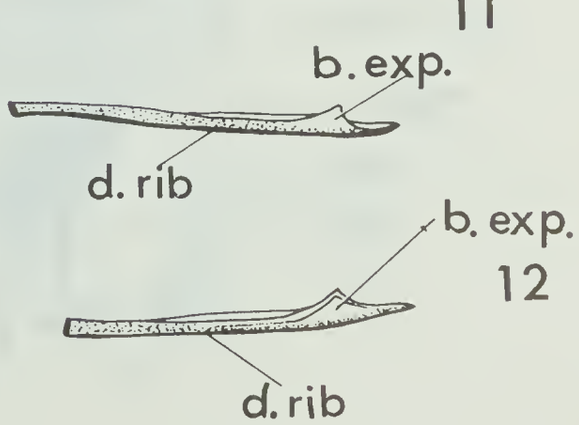
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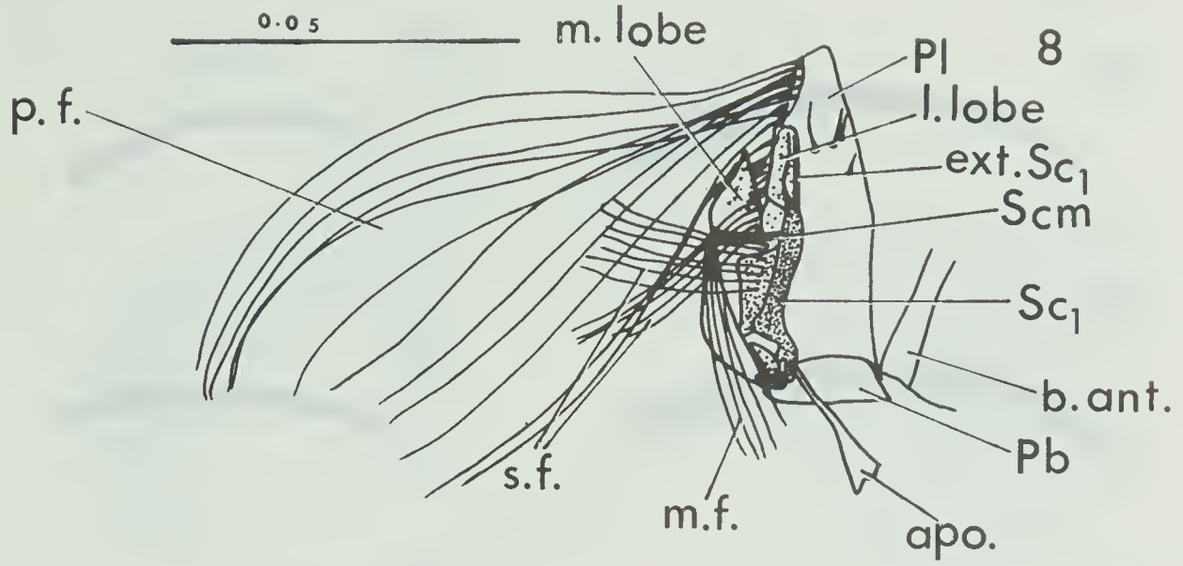
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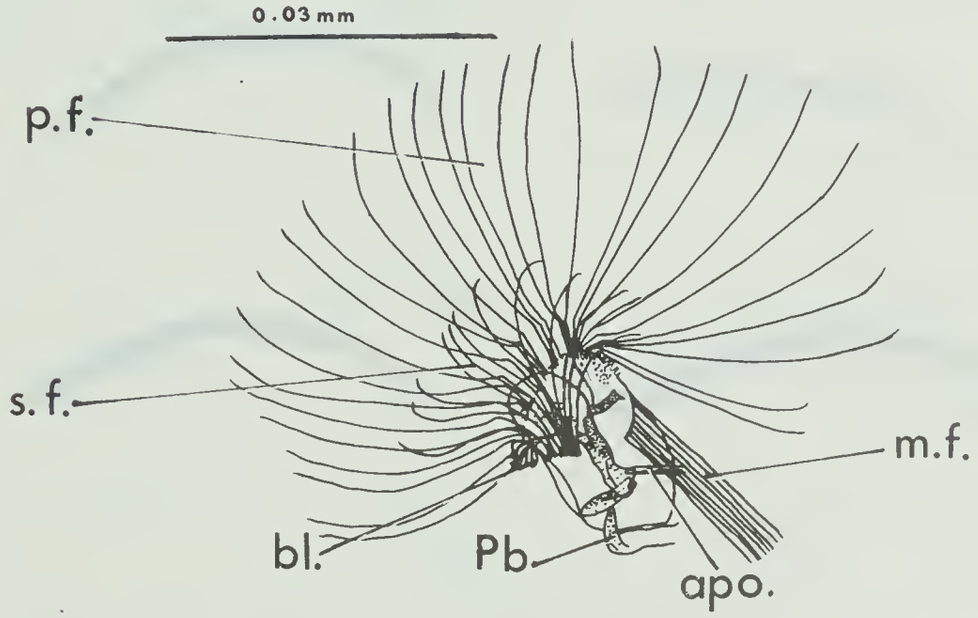
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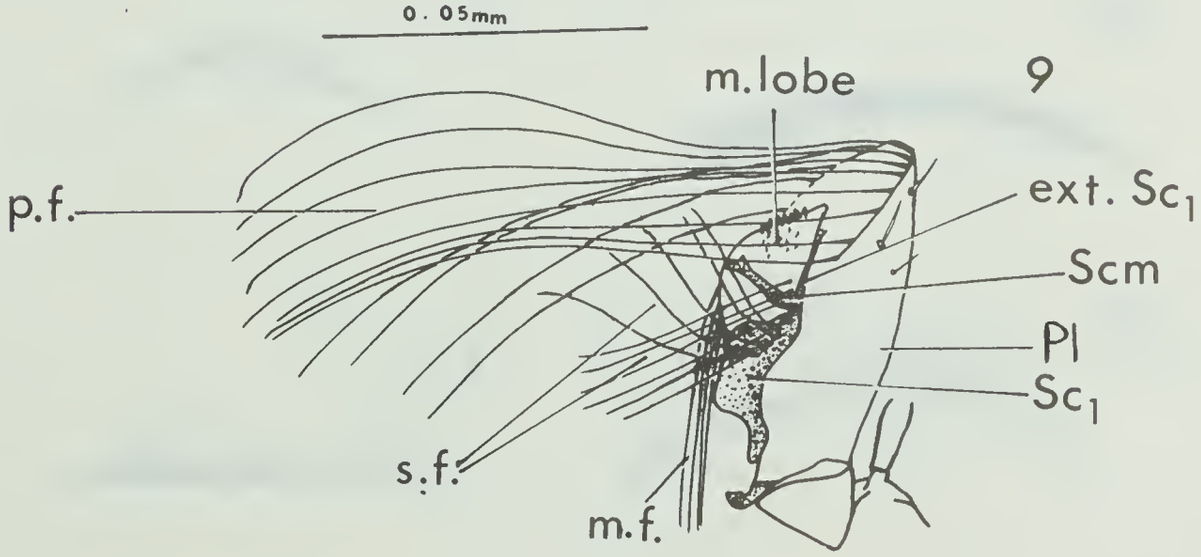
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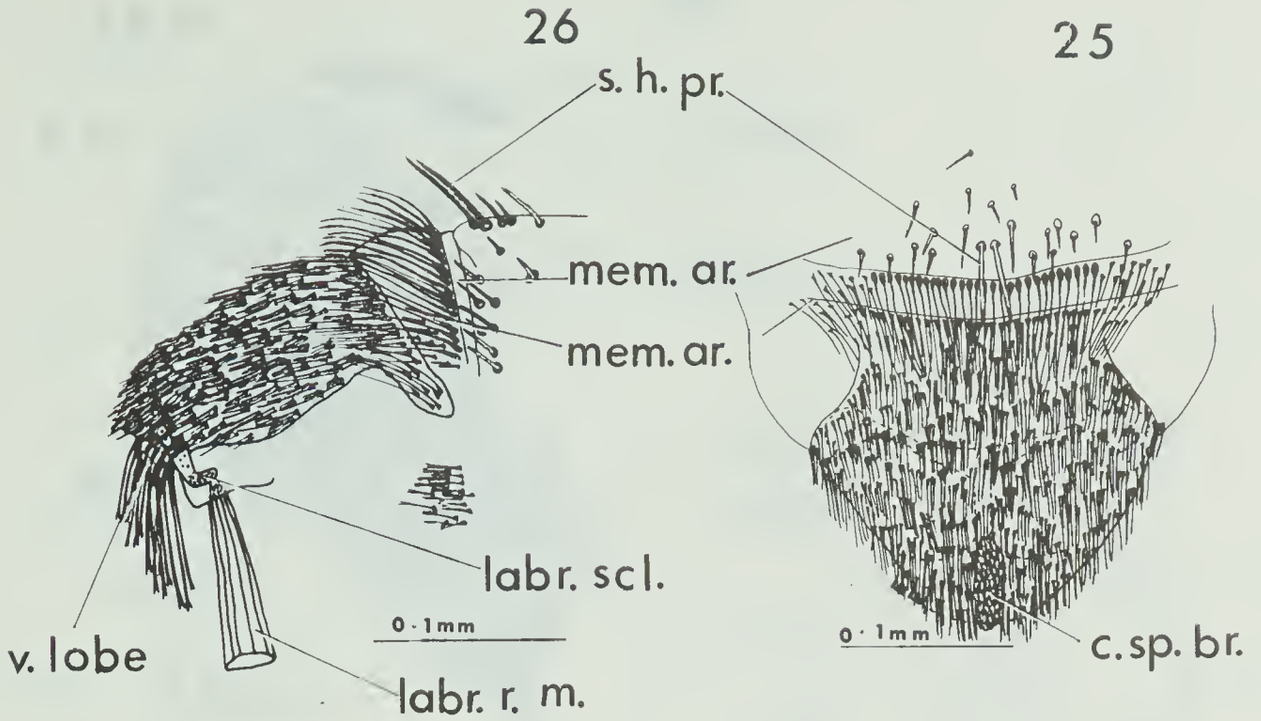
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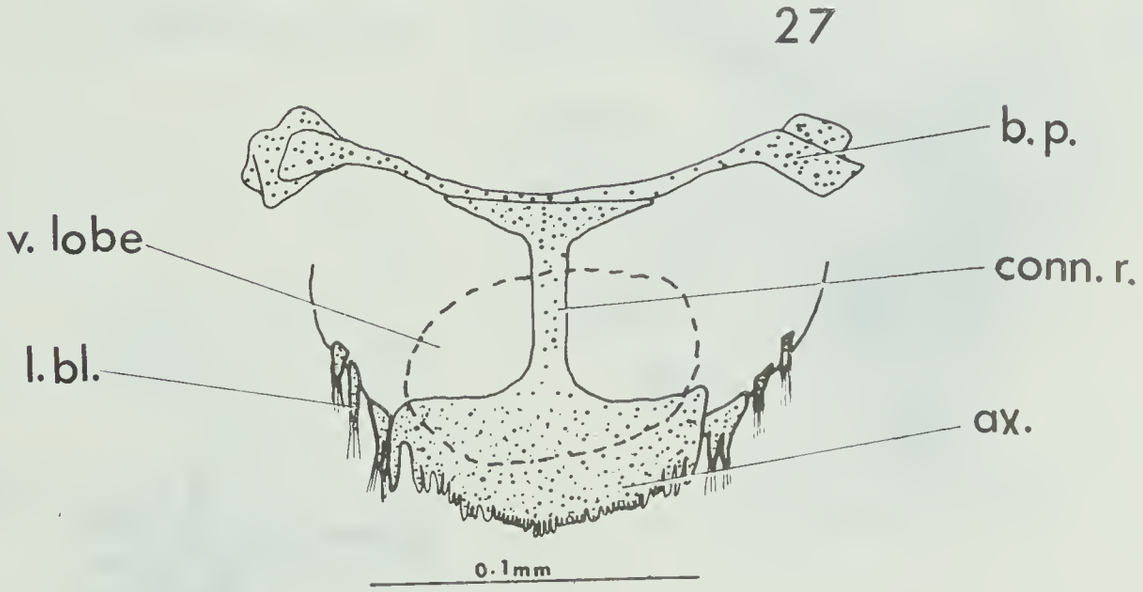
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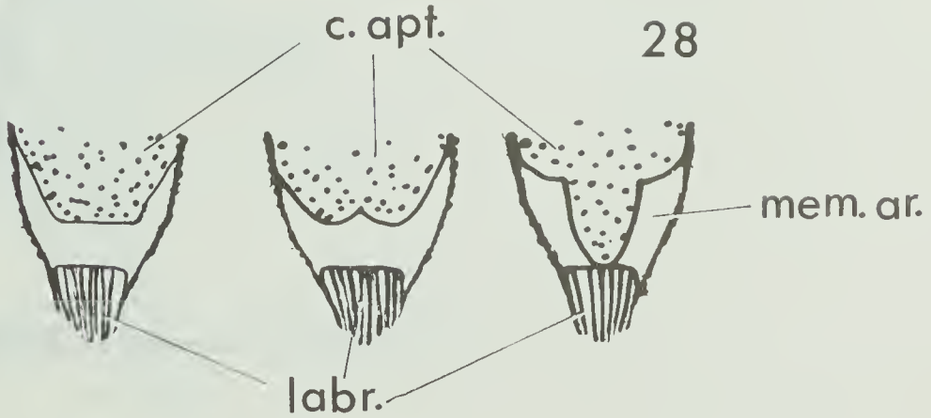
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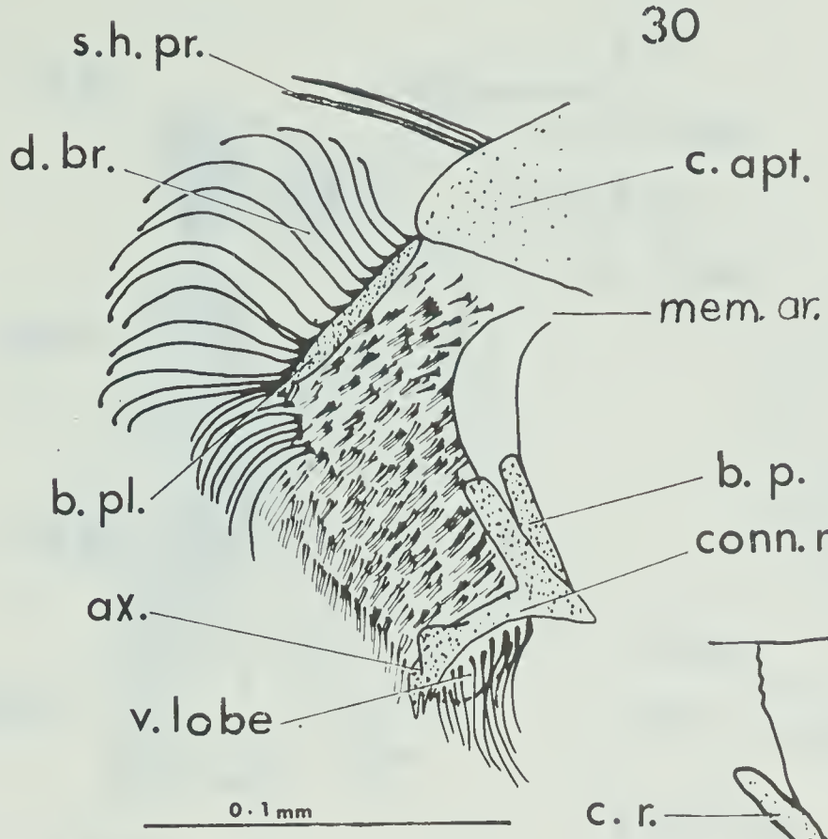
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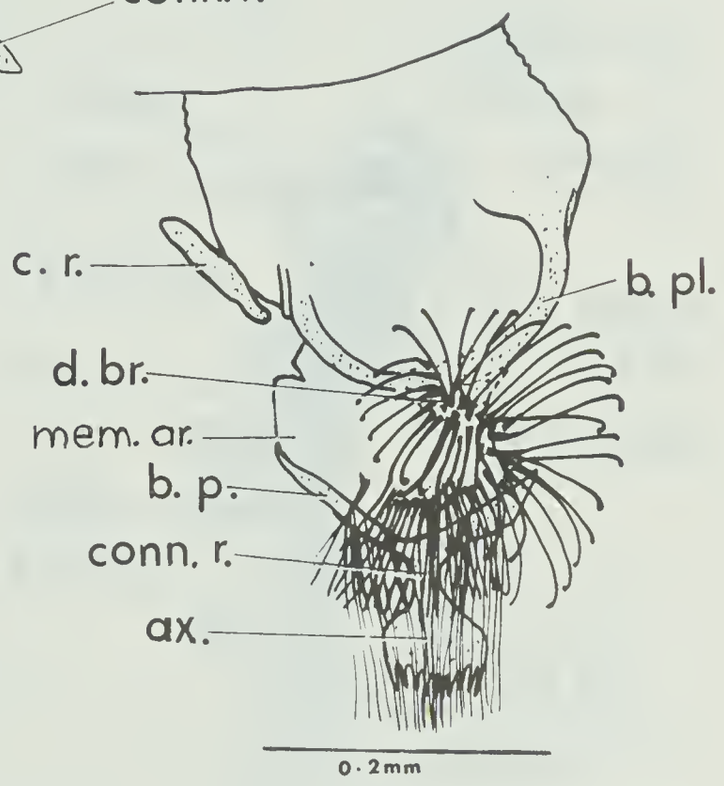
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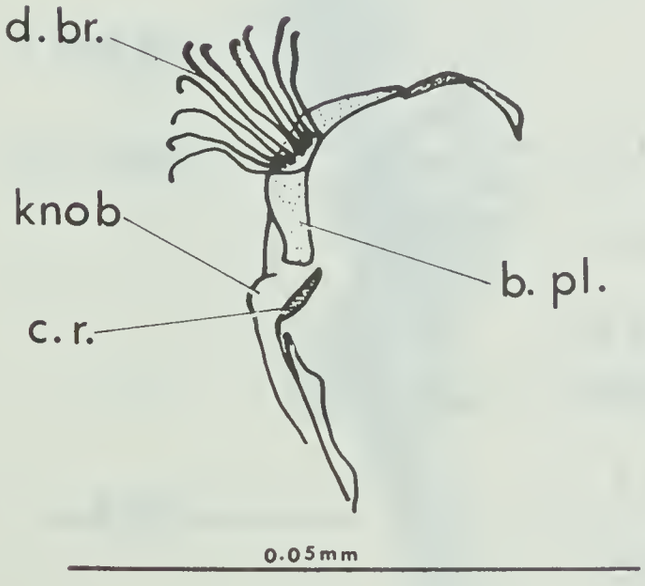
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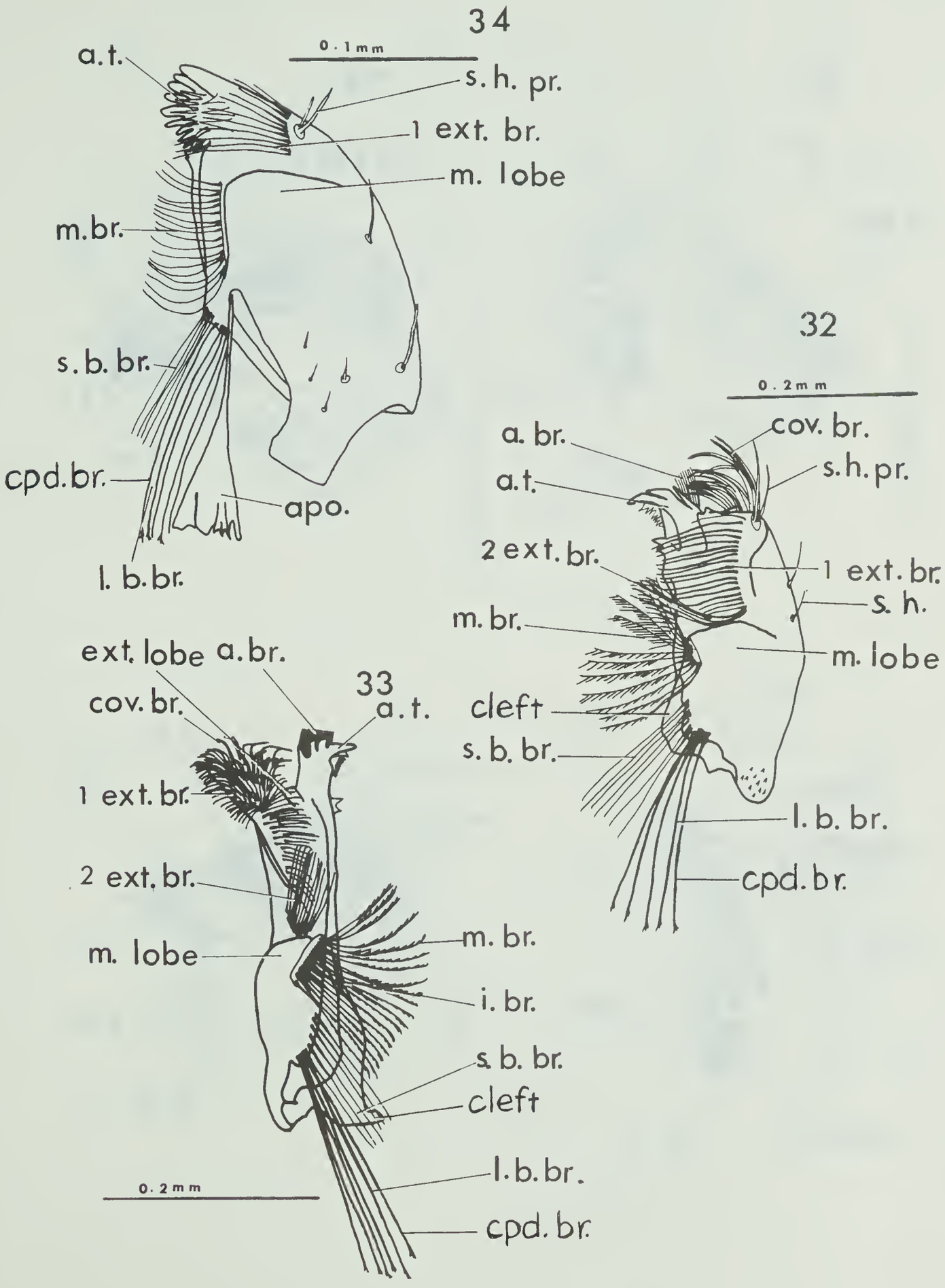
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a.t.
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m. br.
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a. br.
cov. br.
a.t.
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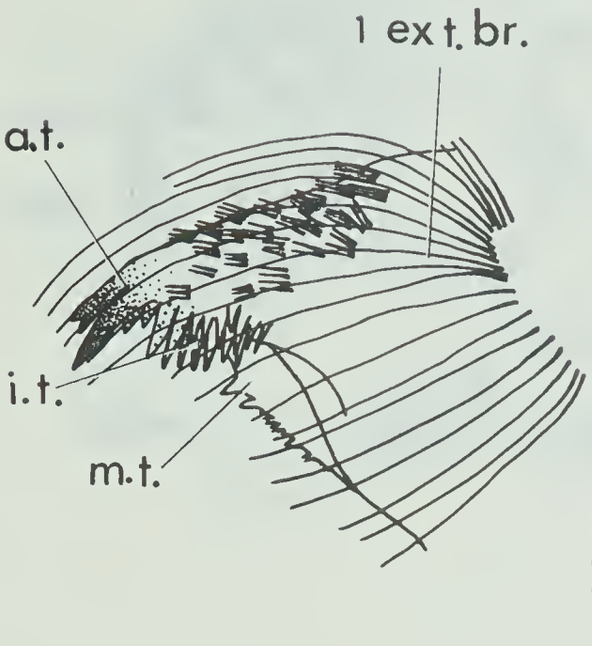
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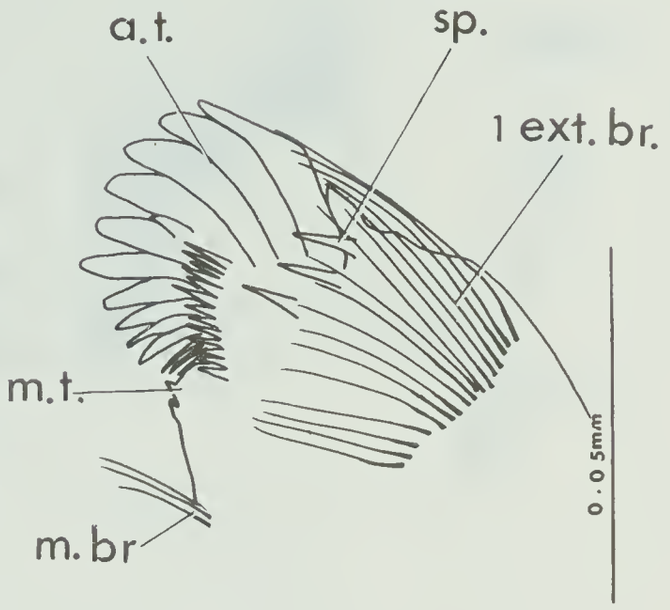
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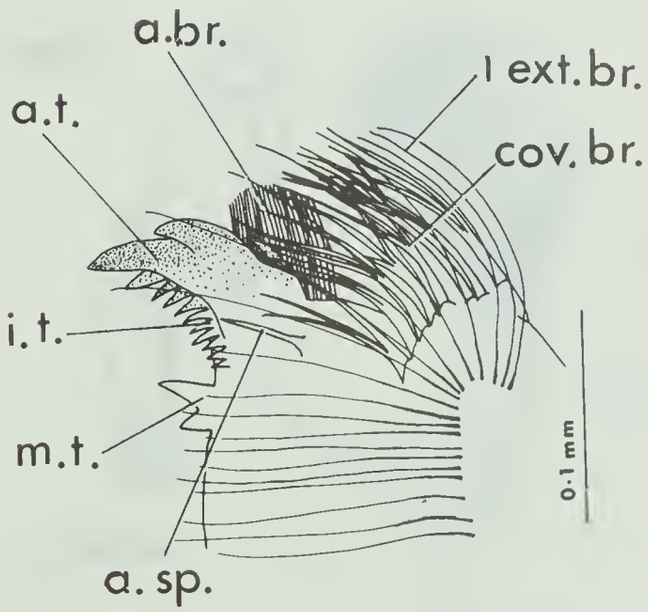
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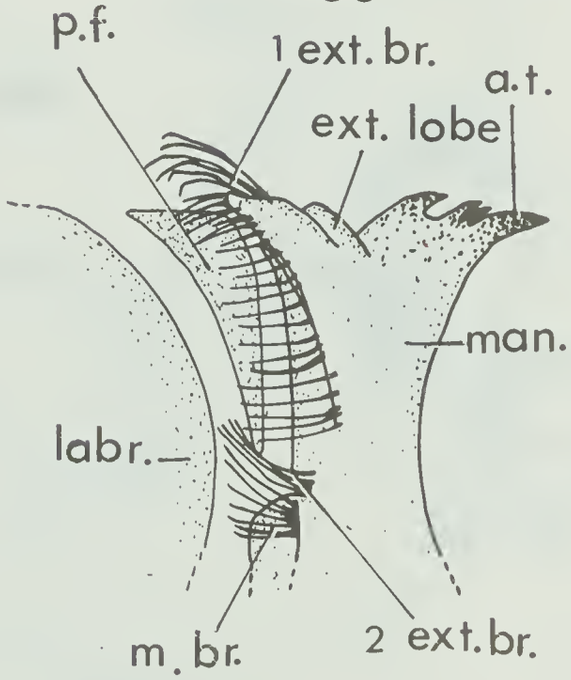
38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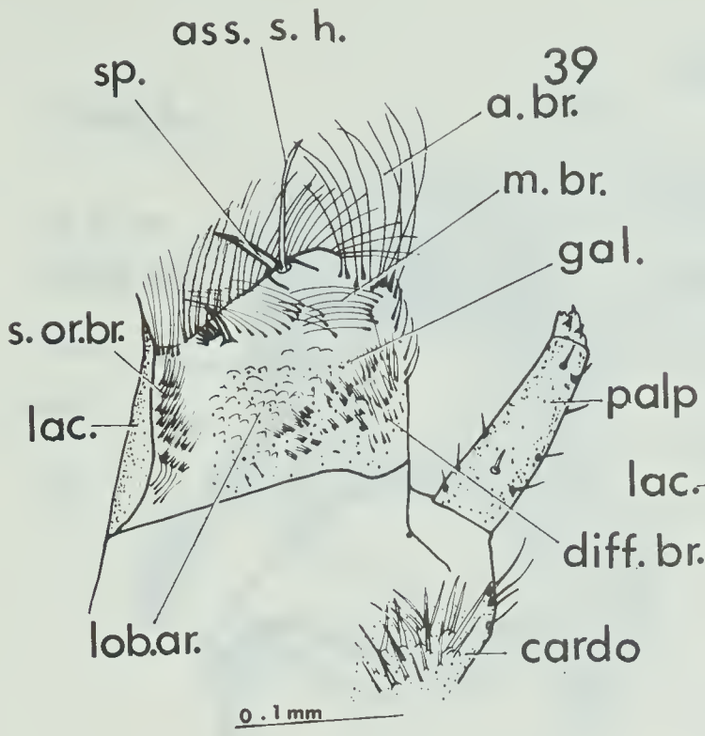
39
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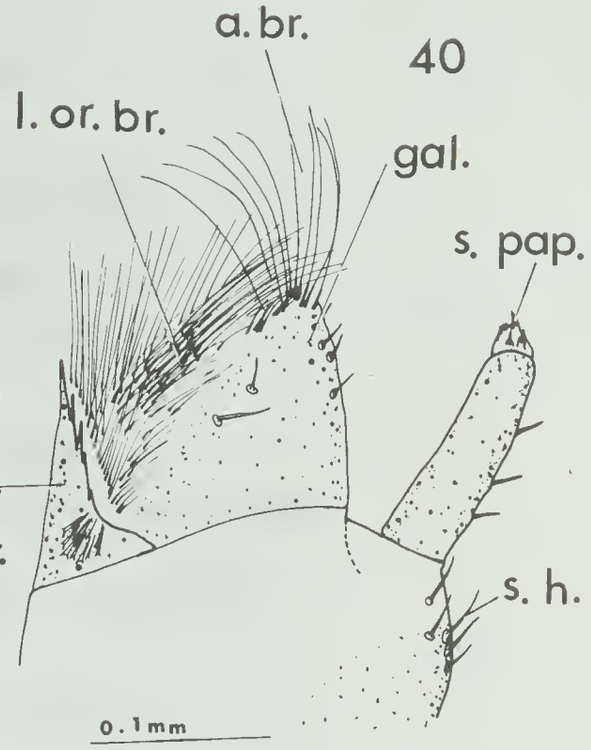
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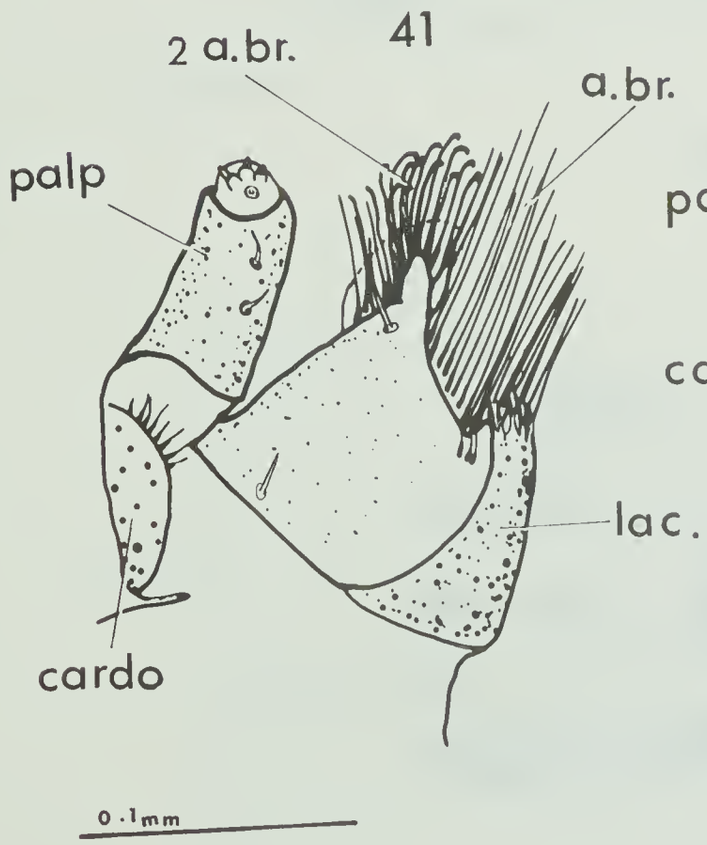
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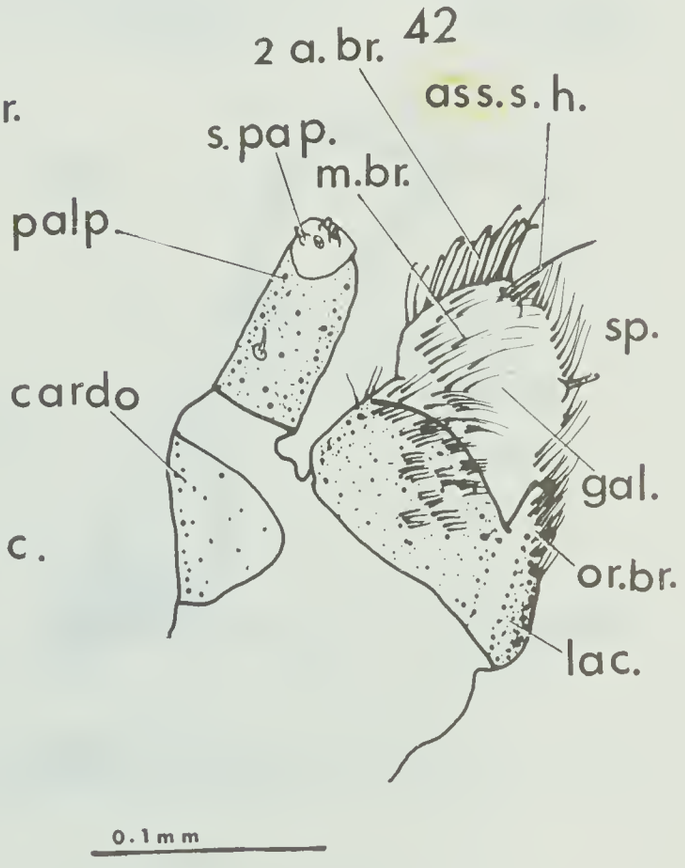
42
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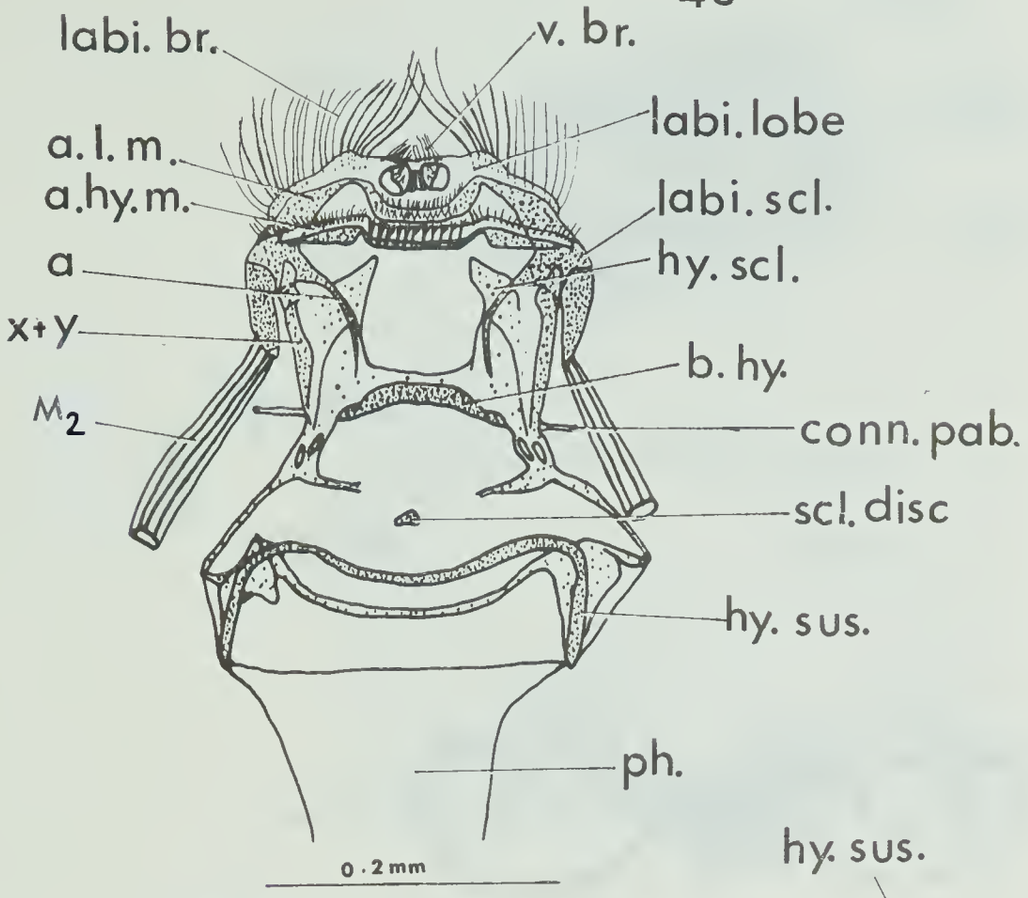
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a
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scl. disc
hy. sus.
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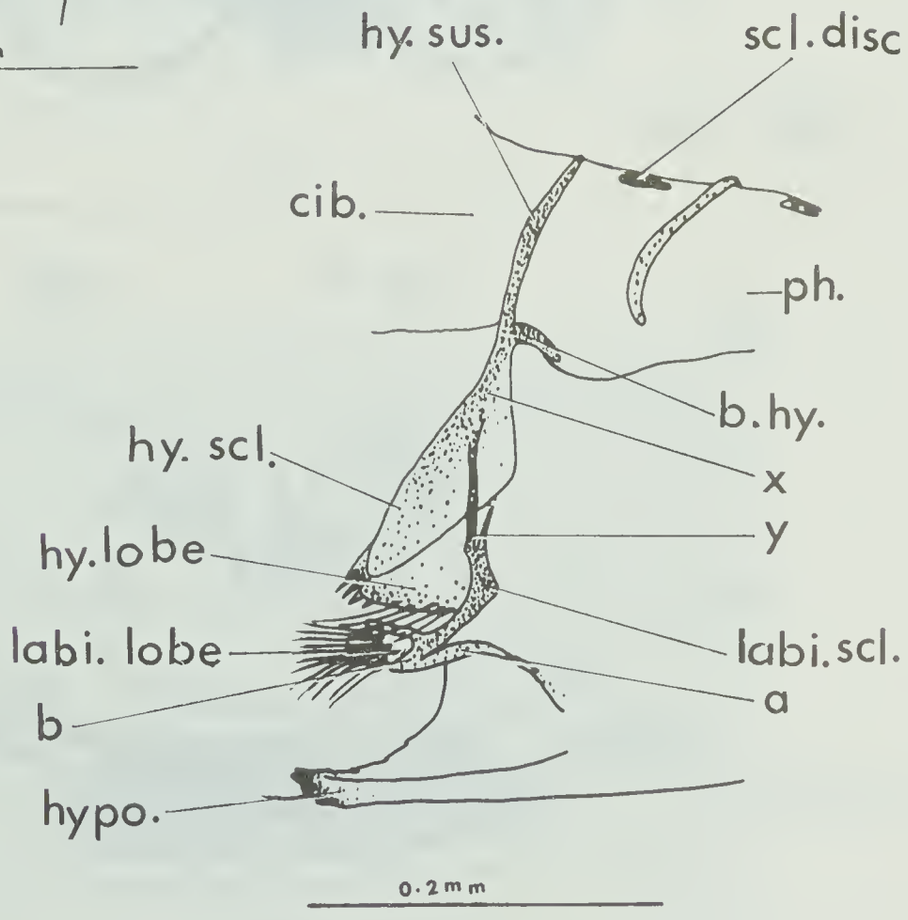
44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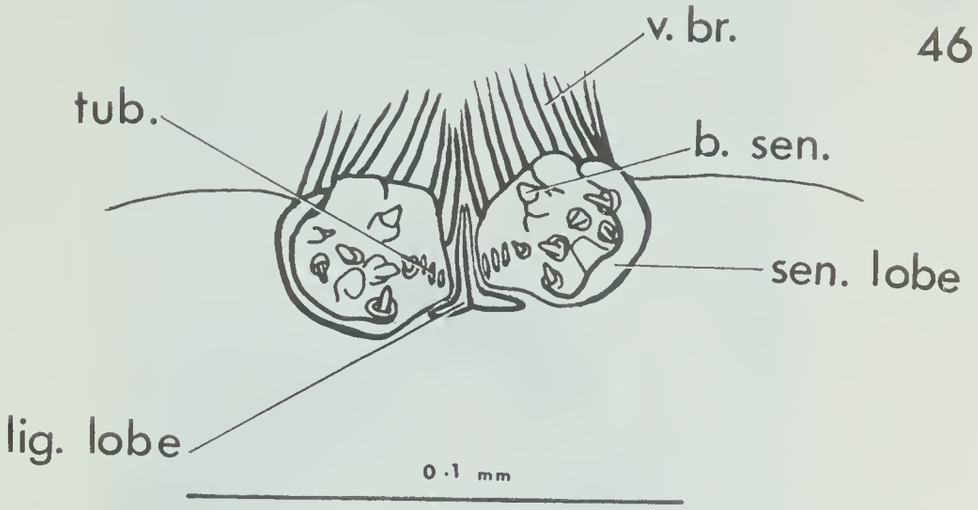
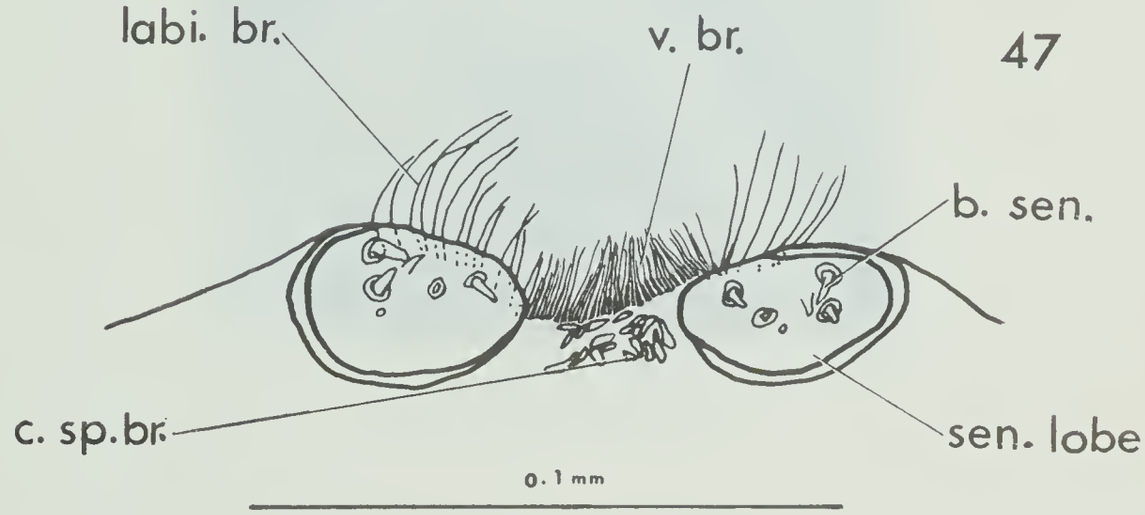

v. br.
tub.
b. sen.
sen. lobe
lig. lobe
0·1 mm

46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v. br.
b. sen.
c. sp.br.
sen. lobe
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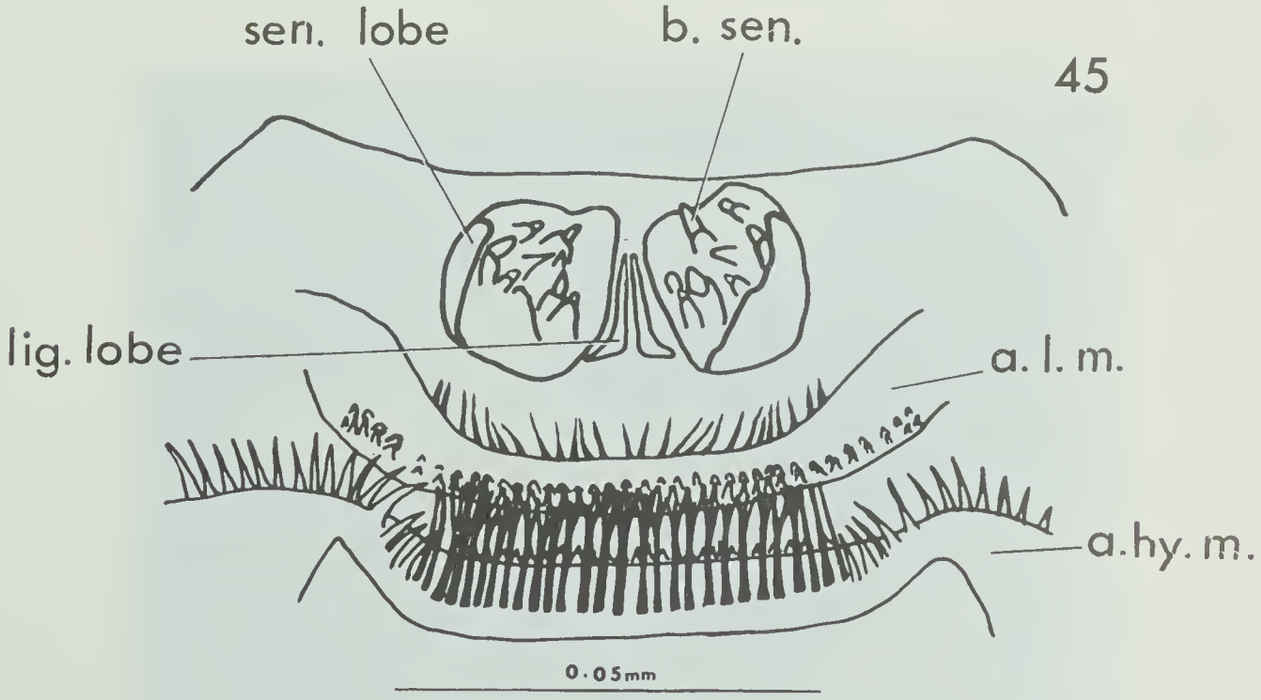
47


sen. lobe
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a. l. m.
a.hy. m.
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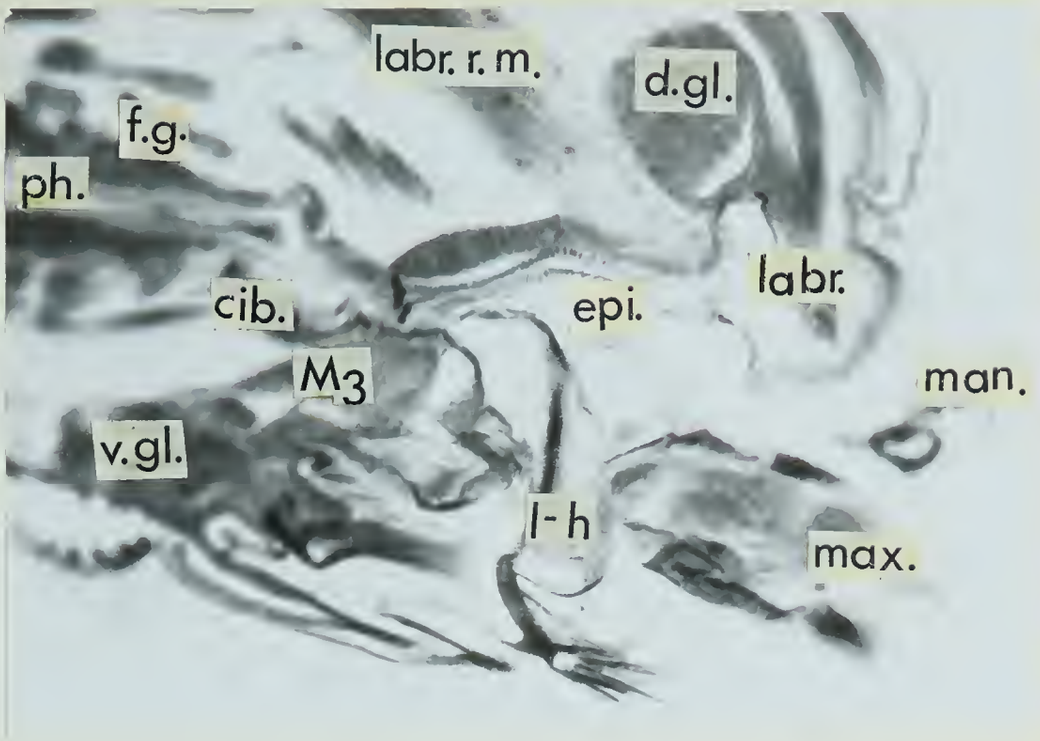
45

48

5μ

2μ

49


labr. r. m.
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epi.
M3
man.
v.gl.
l-h
max.

50

8μ

4μ


d.prj.
M2
v.gl.
sk.can.

51

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8.0. APPENDIX

Table I. Particles ingested by blackfly larvae. Authors of reports listed alongside. Maximum and minimum (when possible) estimates of sizes given in microns (unless otherwise indicated).

Author	Vegetable Food	Size Estimate	Estimate Reference
Miall 1895	desmids		
	diatoms	10 - 20	Jamnback & Frempong-boadu 1966
Kellogg 1901	*Gomphonema* sp.(algae)	4-7 x 12-30 25-6 x 160-135	Tiffany & Britton 1952
	Nitzschia sp. (algae)	2-6 x 32-260	"
		8-14 x 160-500	"
Jobbins-Pomeroy 1916	*Gomphonema* sp. (algae)	4 - 7 x 12 - 30 25-40 x 60-135	"
	Nitzschia sp. (algae)	2 - 6 x 32-260 8 - 14 x 160-500	"
	Vaucheria sp. (algae)	15-33(filament width) 40-123(filament width)	Prescott 1962
	Nothrix sp.		
	Euglena viridis Ehrenberg (algae)	14-20 x 40-65	Tiffany & Britton 1952
	Spirogyra sp. (algae)	21-28 x 210-280 125-150 x 125-500	Prescott 1962
Cameron 1922	*Nitzschia linearis* (Agardi) Wm. Smith (algae)	5 - 6 x 70-180	Tiffany & Britton 1952
	Gomphonema acuminatum Ehrenberg (algae)	5 - 11 x 20-70	"
	Navicula rhynchocephala Kütz (algae)	7 - 10 x 34 - 37	Patrick & Reimer 1966
Puri 1925	diatom shells	10 - 20	Jamnback & Frempong-boadu 1966
	algae		
Wu 1931	diatoms (algae) vegetable matter	10 - 20	"
Metcalf 1932	*Nitzschia* sp. (algae)	2 - 6 x 32-260 8 -14 x 160-500	Tiffany & Britton 1952

Table I (cont'd.).

Author	Vegetable Food	Size Estimate	Estimate Reference
Metcalf 1932	*Gomphonema* sp. (algae)	4 - 7 x 12 - 30 25-40 x 60-135	Tiffany & Britton 1952
	Navicula sp. (algae)	3 - 5 x 4 - 18 35 x 210 - 300	Patrick & Reimer 1966
	Ulothrix sp. (algae)	4 - 6 x 15 20 - 45 x 21-60	"
	Cladophora sp. (algae)	19-74 (filament width) 25-250(filament width)	Prescott 1962
	Vaucheria sp. (algae)	15-33 (filament width) 40-125(filament width)	"
	Conferva sp. (algae)	3 - 6 x 3 - 72 5 - 6 x 10 - 36	Collins 1909
	Scenedesmus sp. (algae)	2 - 5 x 12 - 15 3 - 7 x 30 - 40	Prescott 1962
	Chlamydomonas sp.(algae)	2 - 3 x 3 - 5 15 - 18 x 21 - 29	"
	Euglena sp. (algae)	5 - 10 x 118 - 125 20 - 26 x 250 - 290	"
	Characium sp. (algae)	3 - 6 x 13 - 22 5 - 14 x 80 - 480	Patrick & Reimer 1966
	Spirogyra sp. (algae)	21 - 28 x 210 - 280 125-150 x 125-500	Prescott 1962
	phanerogamous plant fragments		
Smart 1944	debris algae		
Grenier 1949	debris		
	pollen	5 - 200	Faegri & Iversen 1950
	algae		
	diatoms (algae)	10 - 20	Jamnback & Frempong-boadu 1966
	leaf fragments		
Jones 1949b	moss fragments leaf fragments		
	Ulothrix sp. (algae)	4 - 6 x 15 2 - 45 x 21 - 60	Patrick & Reimer 1966
	Ankistrodesmus sp.(algae)	2 - 6 x 25 - 100 2 - 3 x 150	Prescott 1962
	Tolypothrix sp. (algae)		
	Merismo sp.	3 - 5 x 7 - 10 8 - 10 x 10 - 12	"

Table I (cont'd.).

Author	Vegetable Food	Size Estimate	Estimate Reference
	diatoms		
	other algae		
Jones 1950	leaf fragments		
	Closterium sp. (algae)	3 - 6 x 130-206	Tiffany & Britton 1952
		25 - 61 x 50-800	
	Scenedesmus sp. (algae)	2 - 4 x 12 - 15	Prescott 1962
		3 - 7 x 30 - 40	
	Microspora sp. (algae)	5 - 7 x 5 - 7	"
		21 - 27 x 36 - 38	
	other algae		
	diatoms	10 - 20	Jamnback & Frempong-boadu 1966
Jones 1951	dead leaves		
	decaying plants		
Jones 1958	leaf fragments		
	green algae		
	Lemanea sp. (algae)	200-2000 x 1000-40,000	Prescott 1962
	Batrachospernum sp. (algae)	2-5 cm long	"
		12 cm long	
	diatoms	10 - 20	Jamnback & Frempong-boadu 1966
Peterson 1956	*Diatoma heimale* var. *mesodon* (Ehrenberg) Grunow (algae)	6 - 15 x 12 - 40	Patrick & Reimer 1966
	Diatoma sp. (algae)	3 - 5 x 20 - 55	"
		2 - 4 x 40 - 120	
	Navicula sp. (algae)	3 - 4 x 4 - 18	"
		35 x 210 - 300	
	Meridion sp. (algae)	4 - 8 x 12 - 80	"
	Tabellaria sp. (algae)	3 - 4 x 8 - 22	"
		5 - 10 x 25 - 116	
	Cocconeis sp. (algae)	6 - 20 x 11 - 30	"
		12 - 52 x 18 - 63	

Table I (cont'd.).

Author	Vegetable Food	Size Estimate	Estimate Reference
Peterson 1956	*Gomphonema* sp. (algae)	4 - 7 x 12 - 30 25 - 40 x 60 - 135	Tiffany & Britton 1952
	Fragilaria sp. (algae)	2 - 4 x 10 - 40 2 - 4 x 40 - 170	Patrick & Reimer 1966
	Tribonema major		
	Tribonema bombycinum	3 - 6 x 10 - 36	Prescott 1962
	Derbés Solier (algae)	10 - 17 x 15 - 54	
	Oscillatoria sp. (algae)	0.6- 1 x 1 - 3	"
	Chaetophora elegans Roth (algae)	7 - 12 x 15 - 30	"
	Vaucheria sp. (algae)	15 - 33 (filament width) 40 - 125 (filament width)	"
	Spirogyra sp. (algae)	21 - 28 x 210 - 280 125 - 150 x 125 - 500	"
	Basidiomycetes sp. (algae)		
	fungi		
	fungal spores	5 - 50 350 - 1150	Ingold 1965
	fungi mycelium		
	leaf fragments		
	moss rhyzoids		
	pitted vessel elements		
	spiral vessel elements		
	moss leaf fragments		
	decaying fragments		
	conifer wood fragments		
	Hydroamblystegium riparium		
	Hygrohypnume sp.		
Davies & Syme 1958	algae		
	diatoms	10 - 20	Jamnback & Frempong-boadu 1966
	desmids		
	filamentous algae		
Davies 1960	diatoms	10 - 20	"
Anderson & Dicke 1960	diatoms:		

Table I (cont'd.).

Author	Vegetable Food	Size Estimate	Estimate Reference
Anderson & Dicke 1960	*Amphora* sp.	10 - 14 x 16 - 40	Tiffany & Britton 1952
		17 - 63 x 20 - 140	
	Cocconeis sp.	6 - 20x11 - 30	Patrick & Reimer 1966
		12 - 52 x 18 - 63	
	Cyclotella sp.	4 - 10 in diameter	Tiffany & Britton 1952
		6 - 20 in diameter	
	Cymbella sp.	4 - 12 x 15 - 54	"
		20 - 48 x 70 - 265	
	Diatoma sp.	3 - 5 x 20 - 55	Patrick & Reimer 1966
		2 - 4 x 40 - 120	
	Fragilaria sp.	2 - 4 x 10 - 40	"
		2 - 4 x 40 - 170	
	Gomphonema sp.	4 - 7 x 12 - 30	Tiffany & Britton 1952
		25 - 40 x 60 - 135	
	Melosira sp.	3 - 20 x 12 - 17	"
		6 - 38 x 13 - 22	
	Meridion sp.	4 - 8 x 12 - 80	Patrick & Reimer 1966
	Navicula sp.	3 - 4 x 4 - 18	"
		35 x 210 - 300	
	Nitzschia sp.	2 - 6 x 32 - 260	Tiffany & Britton 1952
		8 - 14 x 160 - 500	
	Rhoicosphenia sp.	4 - 8 x 12 - 75	Patrick & Reimer 1966
	Suirella sp.	6 - 15 x 18 - 70	Tiffany & Britton 1952
		40 - 90 x 130 - 435	
	Synedra sp.	1 - 2 x 30 - 162	Patrick & Reimer 1966
		3 - 4 x 4000 - 700	
	algae:		
	Ankistrodesmus sp.	2 - 6 x 25-100	Prescott 1962
		2 - 3 x 150	
	Chlamydomonas sp.	2 - 3 x 3- 5	"
		15 - 18 x 21- 29	
	Coelastrum sp.	8- 20	"
		10 - 12	
	Cryptomonas sp.	5 - 18 x 20- 80	"
		8 - 16 x 15- 32	"
	Euglena sp.	5 - 5 x 118-125	"
		20 - 26 x 250-290	"

Table I (cont'd.).

Author	Vegetable Food	Size Estimate	Estimate Reference
Anderson & Dicke 1960	*Scenedesmus* sp.	2 - 4 x 12- 15 3 - 7 x 30- 40	Prescott 1962
	Radiastrum sp.	9 - 12 in diameter	"
	Trachelomonas sp.	7 - 8 x 12- 13 31 - 44 x 50- 65	"
	Tribonema sp.	3 - 6 x 10- 36 10 - 17 x 15- 54	
	Oocytis sp.	3 - 9 x 7- 20 29 - 40 x 40- 51	"
	Chordatella sp.	2 - 8 x 5- 12 8 - 20 x 13 - 23	"
	Golenkinia sp.	7 - 15 in diameter 15 - 18 in diameter	"
	Spirogyra sp.	21 - 28 x 210-280 125 -150 x 125-500	"
	Cosmarium sp.	10-32 x 22-60 x 9-30 88-100 x 135-169 x 66-69	Tiffany & Britton 1952
	Oscillatoria sp.	0.6- 1 x 0.9- 3 3 - 5 x 12 - 20	Prescott 1962
	Phacus sp.	10 x 24 64 x 111-115	"
	higher plant fragments		
Abdelnur 1968	diatoms (algae)	10 - 20	Jamnback & Frempong-boadu 1966
	algae		
	spores		
	pollen grains	5 - 200	Faegri & Iversen 1950
	decaying fragments		
Maitland & Penny 1967	algae:		
	Navicula sp.	3 - 5 x 4 - 18 35 x210-300	Patrick & Reimer 1966
	Nitzschia sp.	2 - 6 x 32-260 8 -14 x 160-500	Tiffany & Britton 1952
	Asterionella sp.	7 - 8 x 40-130 3 x 20 - 50	Patrick & Reimer 1966

Table I (cont'd.).

Author	Vegetable Food	Size Estimate	Estimate Reference
	desmids		
	leaf fragments		
Fredeen 1960	*Chlamydomonas* sp. (algae)	2 - 3 x 3 - 5	Prescott 1962
	Animal Food:	15 - 18 x 21 - 29	
Miall 1896	some crustacea		
Puri 1925	crustacea fragments		
	chironomid head capsules		
	simuliid larvae head capsules		
Metcalf 1932	isopods	5000-20,000	Pennak 1953
	copepods	300 - 3000 x 2000	"
Smart 1944	debris		
	blackfly larvae		
Grenier 1949	debris		
	rotifers	40 - 2000	Donner 1966
Davies & Syme 1958	half small naid worm		
Maitland & Penny 1960	rotifer eggs		
	chironomid fragments		
	simuliid larvae fragments		
	Miscellaneous:		
Miall 1895	sand		
Cameron 1922	silt		
Metcalf 1932	bacteria		
Grenier 1949	*Polytomella coeca* (bacteria)		
Jones 1949b	gritty debris		
Jones 1950	grit		
Peterson 1966	sand		
Davies & Syme 1958	sand		
	detritus		
Davies 1960	debris		
Anderson & Dicke 1960	inorganic matter		
Abdelnur 1968	soil		
	organic debris		

Table I (cont'd.)

Author	Vegetable Food	Size Estimate	Estimate Reference
Phelps & DeFoliart 1960	parasitic nematodes	13 - 21 x 254 - 277 8 - 15 x 40 - 453	Phelps & DeFoliart 1960
	yeast	1.54	direct measurement
Fredeen 1959	*Bacillus subtilus* Cohnemund Prazmowski	0.3 - 3	Jamnback & Frempong-boadu 1966
	Aerobacter aerogens (Krus) Beijerinck	0.5 - 0.8 x 1 - 2	Breed et al. 1948
	Escheria coli Migula	0.5 x 1 - 3	Breed et al. 1948

Table II. Frequency of retraction of one cephalic fan of *S. vittatum* larvae. * marks larvae with full guts.

No. of flicks		Time (sec.) observed		Frequency (flicks/sec)	
1	1 cont'd	2	2 cont'd	3	3 cont'd
8	20	42.0	20.0	0.19	1.00
13*	20*	150.0	19.2	0.09	1.04
20*	20*	33.6	24.4	0.60	0.82
20*	20*	20.0	50.0	1.00	0.40
20*	100*	26.9	172.4	0.74	0.58
20	100*	59.7	101.8	0.33	0.98
20	27	40.6	20.5	0.49	1.32
20	30	122.0	32.8	0.16	0.91
20	40	60.0	119.5	0.33	0.33
20	48	20.0	60.0	1.00	0.80
20	50	37.0	146.17	0.54	0.34
20	50*	36.0	71.0	0.55	0.70
20	50*	19.5	92.9	1.03	0.54
20	50	35.6	34.5	0.56	1.45
20*	50	14.1	22.0	1.42	2.27
20*	91	16.1	89.6	1.20	1.02
20*	100	18.1	92.0	1.10	1.09
20	100	19.0	139.0	1.05	0.72
20	100*	27.0	92.4	0.74	1.08
20	100*	24.75	138.2	0.81	0.72
20	100*	50.0	108.2	0.40	0.72
20	100*	20.0	172.4	1.00	0.58
20	169*	20.0	300.0	1.00	0.56
20	194*	20.0	300.0	1.00	0.65
20	360*	22.0	300.0	0.91	1.20

Table III. Chi-square values from comparing ingested size distributions of sephadex beads and available size distributions. Based on the data presented in table 7. D. f. for individual chi-square values = 1; for 'sum' values = n-1 where n is the number of different sizes of beads ingested by larvae in each age group. Probability level set at P = 0.05 for which the chi-square value is 3.84. Underlined figures show no significant difference.

Diameter (of bead)	*C. dacotensis* large	*C. dacotensis* medium	*S. decorum* large	*S. venustum* total	*S. vittatum* large	*S. vittatum* medium
25	25.18		795.46	56.67	447.58	932.72
45	53.54		13.21	5.06	13.00	15.66
65	1.34		78.72	0.02	29.21	98.14
85	9.12		45.82	14.00	31.02	41.58
105	3.68		19.13	8.24	0.01	29.73
125	48.20		11.79	0.97	5.72	40.18
145			44.48	56.21	9.56	42.46
165			30.00		40.03	61.38
185			32.88		60.57	81.44
205			13.88		58.99	68.55
225			11.95		49.60	187.13
245			10.62		91.80	
265			10.00		31.47	
285			30.49			
305						
sum	144.07		1147.55	141.17	868.56	1598.97
(G-200)						
25						
45						
65	44.12	271.81				29.27
85		0.87				
105	0.05	3.91				5.90
125	56.14	120.49				4.74
145	10.59	17.50				0.13
165	38.00	293.19				18.00
185	0.53	0.16				18.00
205	57.60	1080.00				54.00
225						1.60
245						
265		4.76				5.56
285						
305						
sum	207.03	1792.69				137.20